THE PARASITES OF MAN.

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THE

PARASITES OF MAN,

AND THE DISEASES WHICH PROCEED FROM THEM.

A TEXT-BOOK FOR STUDENTS AND PRACTITIONERS.

BY

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TRANSLATED FROM THE GERMAN, WITH THE CO-OPERATION OF THE AUTHOR,

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NATURAL HISTORY OF PARASITES IN GENERAL.

SYSTEMATIC ACCOUNT OF THE PARASITES INFESTING MAN.

Protozoa—Cestoda.

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AUTHOR'S PREFACE.

WHEN my permission was asked to publish a Translation of my Work upon Parasites, whieh was just then appearing in a Seeond German Edition, I was the more ready to grant the request, sinee the braneh of Seienee of whieh it treats is one whieh has been eultivated more espeeially upon German soil and by German investigators, but has by no means found in other eountries sueh wide-spread attention as its great seientifie and praetieal importanee render desirable. It is true that English Literature possesses in the Translation of Küehenmeister's Work on Human Parasites, and in the Treatises of Cobbold (Entozoa and Parasites of Man), writings whieh cover the same ground as my own; but Küehenmeister's work is entirely out of date, while Cobbold aims at giving a general sketeh rather than a eomplete delineation of the group.

This, however, is the aim whieh I have kept in view in the eompilation of my book.

I have endeavoured to serve the interests both of the Physieian and the Hygienist, as well as of the Zoologist—the interests of praetiee and of theory, whieh are by no means so diverse as at first sight might appear.

The relations whieh obtain between Parasites and their hosts are in all respeets conditioned by their natural history; and without a detailed knowledge of the organization, the development, and the mode of life of the different speeies, it is impossible to determine the nature and extent of the Pathologieal eonditions to whieh they give rise, and to find means of proteetion against these unweleome guests.

Even small and apparently isolated faets become often of great significanec in this eonneetion, and henee the Physieian eannot afford

to neglect matters which at first sight appear further removed from his department than from that of the Zoologist.

But just as little is it permissible for the latter to forget that the knowledge of the life-history of animals, after which he strives, is to be obtained by the investigation not only of their organization and development, but also of the position which each species occupies in the economy of Nature,—in the present instance of the attitude which the Parasite assumes towards its host.

But few decades have passed since the full extent and the significance of these relationships have been made clear to us. It was only with the introduction of Helminthological experiment that a new path was opened to the field of knowledge, and we Zoologists gratefully recognise that the first impetus to the brilliant discoveries which our science has to show was the work of a Physician, and we rejoice that at the present day Medicine takes an active part in the prosecution of these studies. This partnership in the work ensures further progress in the future, which is the more important, since our knowledge of the Parasites of Man in particular has in no respect reached a satisfactory condition. Numerous weighty questions still await their final solution.

As to the part which I have personally taken in the cultivation of the science, it may be passed over with the remark that I have devoted my labours to it for a period of more than thirty years. If my efforts have in many respects been crowned with success, I owe it mainly to the long period during which I have followed up the solution of the problems in hand. The number of animals used for Helminthological experiments amounts to many hundreds, and much larger is the sum of the Parasites investigated.

What I offer to my readers, then, is the result of a prolonged and minute investigation, and my work contains little which does not rest upon the basis of personal observation.

Although my book is devoted mainly to the Entozoa infesting Man, it offers an almost complete survey over the present state of that part of Zoology which treats of Parasites. The first section

contains a general natural history of these remarkable animals, intended to give a clear exposition of the phenomena of Parasitic life in its various forms, as well as to narrate the history of our knowledge of them. And similarly there is prefixed to the special account of the various species a general sketch of the structure and life-history of the groups to which they belong. This course was adopted not only for purely scientific reasons, not only in order that the individual facts might be fully treated in connection with related phenomena, but also because by this means alone was it possible to supply, by well-grounded hypothesis and inductive reasoning, the gaps in our experience. The basis of our knowledge must be as extensive and as profound as possible, in order that the origin and nature of Parasites may be treated clearly and satisfactorily.

By this mode of dealing with the subject I hope to have met the wants of those who are actuated by no interest in the Parasites of Man in particular. Here I refer chiefly to the Veterinary Surgeon and Cattle Breeder, who, in a summary of all that is known regarding the life-history of Parasites, will find the means of becoming more closely acquainted with those specially important Entozoa of our Domestic Animals which also infest Man.

In leaving out of consideration the Therapeutic treatment of Parasitic Diseases, I have followed the advice of one of our greatest medical authorities, and I did so the more readily, since, owing to the lack of personal experience in this matter, I could only have recapitulated the works of others. Correspondingly greater prominence has, however, been given to those Hygienic principles which the study of Parasites gives us for the protection of society and its material interests, and which demand the more attention since they have hitherto been insufficiently practised. It is in this connection that the importance of modern Helminthology is most conspicuous; for nowhere is it more true that "prevention is better than cure," than in the case of Parasitic Diseases. It is sufficient to point, by way of illustration, to the Hydatid Tumours, Liver-Rot, and Trichinosis.

In spite of the importance attributed to the medicinal aspects of

the question, it was no part of my plan to make the book into a collection of Pathological curiosities, by the detailed narration of numerous cases. Those who desire such a record are referred to the pages of Davaine, "Traité des entozoaires et des maladies vermineuses,"—a work which only partially justifies its title, since the Zoological portion is very incomplete, and by no means up to the level of our present Helminthological knowledge.

In conclusion, I must point out that the earlier sheets of the German Edition of this volume have already been published six years, in the course of which investigation has been active, and much has been added to our sum of knowledge. Whilst revising the present translation, I have striven, by the addition of notes and by modifications of the text, to give an account of this progress, and hope that nothing of importance has been omitted.

In the original compilation of this work I thought primarily of German readers, and hence it bears throughout traces of its origin. But the quiet activity of the man of science is everywhere a portion of the universal work of that spirit whence the history of culture took its origin, and so may my book for the profit of the whole pass over the bounds of its home, and win for itself new friends in other lands!

In conclusion, it affords me very great pleasure to express my hearty thanks to Mr. W. E. Hoyle, the Translator of my work, for the conscientious and in every way satisfactory manner in which the English Edition has been prepared.

RUDOLF LEUCKART.

LEIPZIG, *September* 1886.

TRANSLATOR'S PREFACE.

The present translation was undertaken, in the first instance, by my friend and former colleague Mr. F. E. Beddard, who found, on his appointment to the Prosectorship of the Zoological Society, that his leisure was insufficient to allow of his completing the work, and therefore made the proposal that I should carry it forward. The manuscript which he had already prepared was handed to me, and contained an admirable rendering of the first half-dozen sheets, which, with few modifications, is here reproduced.

As regards my own share of the work, but little needs to be said: not even those reviewers who so persistently, and in many cases so reasonably, decry the translation of German text-books, will require an apology for an attempt to render more widely known in this country a work which has long since attained the rank of a classic in its native land.

No pains have been spared to present the English reader with a faithful rendering of the original; and the supervision which the Author has exercised over the proof-sheets not only furnishes a guarantee that he has not been misrepresented, but has also rendered it unnecessary for me to do anything in the way of bringing the work up to the times. A number of passages which in the course of time had become antiquated were cut out by the Author, who also supplied other paragraphs containing the results of more recent researches. These have all been placed in brackets, and are followed by the initials of the Author. The few additional remarks which I have thought it necessary to make are in all cases indicated by my own initials.

Thanks to the writings of Cobbold and others, our language already possesses equivalents for most of the technical terms in this work, but it has always appeared to me that it would be very desirable to distinguish between the transference of a parasite from one host to another, and its movement from one organ to another in the same host. Hitherto the word "migration" has been used in both these senses, but in the present work I have confined it entirely to the former signification, and adopted "wandering" to express the passage from one organ to another.

The Second Volume of the original is now being revised by the Author, preparatory to the issue of a new edition; he has kindly undertaken to forward the proof sheets of this for translation, so that the English version may pass through the press *pari passu* with the German, and be published simultaneously with it.

In conclusion, I must fulfil the pleasant duty of expressing my great indebtedness to my friend Mr. J. Arthur Thomson, M.A., who has acted as my assistant throughout the progress of the work. Upon him much of the more laborious part of the work has fallen, and without his painstaking and intelligent co-operation the present translation could not possibly have been completed in the time which has elapsed since it was undertaken.

WILLIAM E. HOYLE.

CONTENTS.

SECTION I.

NATURAL HISTORY OF PARASITES IN GENERAL.

CHAPTER I.

NATURE AND ORGANIZATION OF PARASITES.

CHAPTER II.

OCCURRENCE OF PARASITES.

CHAPTER III.

THEORY OF THE ORIGIN OF PARASITES REGARDED HISTORICALLY.

CHAPTER IV.

LIFE-HISTORY OF PARASITES.

CHAPTER V.

THE ORIGIN OF PARASITES,

AND THE GRADUAL DEVELOPMENT OF PARASITIC LIFE.

CHAPTER VI.

THE EFFECTS OF PARASITES ON THEIR HOSTS,

PARASITIC DISEASES.

SECTION II.

SYSTEMATIC ACCOUNT OF THE PARASITES INFESTING MAN.

INTRODUCTION.

LIST OF ILLUSTRATIONS.

SECTION I.

NATURAL HISTORY

OF

PARASITES IN GENERAL.

CHAPTER I.

NATURE AND ORGANIZATION OF PARASITES.

THE term "Parasite," in its widest sense, includes all those creatures which inhabit a living organism, and obtain nourishment from its body.

This definition includes not only vegetable and animal parasites (phytoparasites and zooparasites), but also parasites on plants and on animals. The larva that inhabits the wood of a tree or the pulp of a fruit is to be regarded as a parasite in no less degree than the thread-worm of the human intestine; and the beetle that defoliates our forests is quite as much a parasite as the louse upon the feathers of the swallow. Parasitic life, then, as thus understood, is an exceedingly widespread phenomenon.

So long as the term "parasite" was confined to certain special forms, as was the case formerly, it followed as a necessary consequence that parasitism was an isolated phenomenon, and bore no relation to any other mode of existence. Now, however, this view is known to be false, a matter of great importance when we come to study the subject from a historic point of view. It is not merely the intestinal worms and allied forms that are to be included among parasites, but also numerous creatures that sometimes resemble so completely certain free-living animals, except in the nature of their food, that an independent mode of existence has been actually ascribed to them. Does it correspond with the common view of the peculiar nature of parasitism, that a creature which, according to the definition just given, ought to be regarded as a parasite, should be sharply distinguished from another free-living animal simply because it feeds upon a living branch instead of dead wood, or on green foliage instead of withered leaves? Do not the value and meaning of these differences appear less than those which obtain between carnivorous animals on the one hand and herbivorous on the other?

The question raised here remains the same, when we limit more narrowly the conception of parasitism, which on practical grounds is advisable for the purpose of this work, and confine it entirely to *animals living as parasites upon other animals.*

Under this limitation, the group of parasites appears at first sight to be considerably more restricted than it did from the former wider point of view, and in earlier days, when it was thought that parasites always existed as parasites, for the simple reason that they were unable to lead a free existence, even more restricted than now.

Modern investigations have taught us that there are frequently stages in the existence even of the most thorough-going parasites, such as the intestinal worms, when they lead a free life in water or damp earth; and also that among the thread-worms there are many species (*e.g., Rhabditis*) that are occasionally parasitic, and capable of arriving at their full development in milk, meat, and other organic substances as rapidly as, if not more quickly than, in the interior of a living organism. In another thread-worm (*Ascaris nigrovenosa*, Auct.), we have an instance of an animal whose life-history consists of two alternate generations,[1] both sexually mature, which differ so much from each other in structure and mode of life, that, before their genetic connection had been discovered, they were referred to two distinct families.[2] This case, which has such an important bearing upon the meaning and right understanding of the phenomenon of parasitism, will be described more fully in a subsequent chapter.[3] It follows, therefore, from a case like this, that certain animals, such as the larvæ of many flies (*Musca vomitoria, Sarcophaga carnaria, Anthomyia canicularis*, &c.), which occasionally feed upon living animals, although usually found in dead putrifying organic matter, are by no means to be excluded from the category of parasites. If this kind of parasitism is to be distinguished in any way, it may conveniently be termed "occasional," in contrast to the "constant" parasitism exhibited by other animals. The term "pseudoparasite," which has been frequently, even in recent times, applied to cases of this kind, ought to be confined to various objects, such as hairs, vegetable tissue, &c., which have been mistaken for parasites, and even described as such;[4]

[1] For a fuller account see Vol. II.

[2] The case mentioned in the text is not the only one known. Recent investigations have shown me that *Anguillula stercoralis*, occurring in cases of "Cochin-China diarrhœa," is the Rhabditiform generation of *A. intestinalis* (Leuckart, *Bericht math. phys. Cl. k. Sächs. Gesellsch. d. Wiss.*, p. 85, 1882). There lives also in the peritoneal cavity of *Hylobius pini* a strange parasite, *Allantonema mirabile*, Lkt., whose offspring leads a free existence, and gives rise to many generations of *Rhabditis*, like sexually mature worms (Leuckart, *Tagebl. d. Magdeburg. Naturf. Versamml.*, p. 320, 1880.—R. L.

[3] Chapter VIII.

[4] A list of this kind of pseudoparasites, including only the commonest, would be too long for insertion here. It may be remarked that all kinds of objects, not only the *débris* of food (orange-pips, raisin-stones, sinews, small bones, and so forth), but also pieces of thread, hairs, &c., have been mistaken for parasites. It is generally not difficult to distinguish these by the help of the microscope.

and, in my opinion, also for frogs, snakes, and spiders,[1] which have been stated by many authors to have existed for years in the human alimentary canal, although it is perfectly certain that animals of this kind cannot endure the damp heat of the body of a mammal for more than six hours.[2]

This occasional parasitism sufficiently points out what has just been maintained from another point of view, that no broad line of demarcation can be drawn between parasites and free-living animals.

It is not, however, in such instances alone that the transition between the free and parasitic modes of existence is found. Many animals (such as the leech) are only parasites so long as they obtain their nourishment at the expense of larger and more powerful creatures, becoming simply carnivorous when they prey upon other animals of their own size or smaller. A parasite is, in all cases, smaller and weaker than the animal on which it feeds. Being incapable, therefore, of overpowering it, the parasite contents itself with plundering its host and drawing nourishment from its juices and flesh.

Thus the parasitic and free modes of existence are related to each other in two distinct ways, both of which are connected with peculiarities of parasitism itself, one of these links being *the nature of the food,* the other *the relation of the parasite to the animal which supplies the nourishment.* Reflecting upon the significance, already pointed out, which the size and equipment of the parasites have with regard to their mode of life, it is not surprising that the various groups of the animal kingdom do not all furnish equal contingents to the army of parasites. Among the Vertebrata, for instance—the majority of which are strong and of large size—there are very few parasitic forms; while, on the other hand, among the comparatively small and feeble Arthropoda and worms there are entire families, all, or nearly all, the members of which lead a parasitic life. In fact, it may safely be asserted that these two groups contribute more parasitic forms than all the other divisions of the animal kingdom taken together.

[1] In these cases, also, the microscope serves to dispel the illusion; for the contents of the intestines of these pseudoparasites will contain substances that could not possibly have been obtained in the body of their host. In estimating the origin of various objects asserted to have been evacuated by a patient it is impossible to be too careful. In such cases there is frequently an attempt to deceive the medical man, but more usually some error has been introduced through a variety of circumstances. If, for instance, everything that is found mixed with the fæces be, without further investigation, set down as having come from the body of the patient, then the famous helminthologist, Dr. Bremser, must have evacuated, as he humorously relates, a pair of snuffers; for they were certainly found in the bed-pan at a time when he was slightly indisposed, without any one having placed them there.

[2] Berthold, "Ueber lebende Amphibien im lebenden Körper," *Müller's Archiv f. Anat. u. Physiol.*, p. 430, 1849.

The parasites of man and the higher vertebrates belong exclusively to them.

Comparing together the various forms of animal life included here in the group of parasites, we find numerous and striking differences, not only in structure,—which corresponds of course to their zoological position,—but also in their biological aspects—*in the nature and degree of the parasitism exhibited.* On the one hand, there are parasites which only occasionally seek out their host, and only remain long enough to take in a sufficient supply of food, departing as soon as this is done, and subsequently, perhaps, seeking out a fresh host. On the other hand, there are parasites that pass a considerable time, perhaps a whole stage of their existence, in the body of their host, which thus serves as a dwelling-place as well as a source of nutriment. This difference may perhaps be best expressed by the terms "temporary" and "stationary;" but it must be pointed out that between these two kinds of parasitism no absolute line of demarcation can be drawn, any more than between the parasitic and free modes of existence; the terms, however, may be retained, as they express two degrees of parasitism, which are, generally speaking, sufficiently distinct and are sometimes widely separated from each other.

Even among the older zoologists this distinction was recognised, but "temporary" parasitism was usually so called in contradistinction to life-long, instead of to merely "stationary" parasitism. At that time, however, the fact that even the most thorough-going parasites—the intestinal worms—are free during part of their life, was not known, and, accordingly, the contrast implied between the types of parasites was different altogether from that put forward here. Besides those parasites which exist as such throughout their whole life-cycle, there are others which lead a free life for a longer or shorter period, either in the adult condition (ichneumon-flies and gad-flies), or as larvæ (certain thread-worms).

"Stationary" parasitism, therefore, manifests itself in two ways; it may be (1) "permanent," lasting for life; or (2) "periodic," embracing only a stage in the life-cycle, and therefore involving at some time or other a change from parasitic to free life.

The various kinds of parasitism just enumerated possess an interest and importance that depend not merely upon their relations to each other and to other modes of existence; they are interesting also from the fact of the influence which they have in modifying the structure of the body, so that an examination of any form of parasite enables one to foretell with moderate certainty the particular kind of parasitism which it exhibits. Thus, temporary parasites must evidently be provided with the means of approaching and abandoning

their host; they must have organs of motion and of sense. This is invariably found to be the case; temporary parasites possess powerful limbs (*e.g.*, the bed-bug), sometimes even wings (midges and some other flies[1]), or swimming appendages (fish-louse). When present, these organs allow of a more complex development of the vital activities, and that, perhaps, to such a degree, that temporary parasites, when away from their host, display hardly any recognisable peculiarities. Only the nature of their food, and the way in which they obtain it, compel us to regard them as parasites; it is not the refuse of organic life, but living organisms, that supply them with nutriment.

As the power of movement becomes less, it becomes more and more difficult for the parasite to leave its host. In this way a temporary gradually changes into a stationary parasitism; the host which was formerly only visited at intervals, and for a short time, now serves as a shelter to the parasite, and is seldom abandoned by it or changed for another. Among stationary parasites there are many (*e.g.*, the flea) which retain the power of movement, and sometimes abandon one host for another in search of a safer dwelling-place or more abundant nutriment. These forms present many analogies to the temporary parasites, not merely as regards their mode of life, but in their structure, especially in regard to the development of locomotor organs. In the majority of cases, however, the power of movement is reduced in stationary parasites, sometimes entirely lost, so that the animal remains for months, or even years, attached to the same host. Instances of this may be found in the bladder-worms and the female Lernæadæ, which live with their heads imbedded in the muscles of fish. Moreover, it is not only the organs of locomotion which become abortive in these cases. The sense organs, and especially the eyes, whose development is almost co-extensive with the variety and energy of the muscular activity, in like manner frequently degenerate. The graceful outline of the body and its segmentation commonly disappear, in adaptation to the present slight need of locomotion.

In fact, a glance at the group of the so-called intestinal worms, which are all stationary parasites, shows clearly *that the more sedentary the life of a parasite becomes, the simpler and more undifferentiated is the form of the body.*

Moreover, the simplification of the external structure of the body is no more a special peculiarity of stationary parasites than is the possession of wings and swimming feet a peculiarity of free-living animals. Among the latter we find numerous examples of a similar form of body, and especially among those creatures with limited capabilities of locomotion, which, in this respect, are somewhat

[1] *Hippobosca*, *Ornithomyia*, &c.

analogous to stationary parasites. I only need to mention certain caterpillars and other insect larvæ, many of which lead a stationary life like the intestinal worms, and, furthermore, resemble them in that, in many cases (*e.g.*, ichneumon-flies, &c.), they are occasionally or even constantly parasitic. Besides these negative characters, stationary parasites can in many cases be recognised by positive characters, such as the possession of hooks and suckers, which serve to fix them on to the body of their host. Structures of this kind are by no means confined to stationary parasites, but are also commonly found in temporary parasites, and occasionally even in free-living animals, where, however, they are never so conspicuous or so constantly developed. The more the power of locomotion in a parasite diminishes, the more difficult it is for it to migrate to another animal, and it must therefore be provided with organs which will enable it to retain its position under the most adverse circumstances. These organs of attachment vary in character, in correspondence with the structure of that part of the body of the host upon which the parasite dwells,—being generally stronger and larger in those forms which are parasitic upon the outer skin than in those which live in the interior of the body of their host. Among internal parasites, again, the organs of attachment are generally more developed in those species which live in the alimentary canal, since they have to withstand the pressure of its contents. Many intestinal worms, however, do not possess any hooks or other organs of attachment; but in these cases there is generally some compensation. Among the thread-worms, for example, which we shall presently consider, the form and length of the body seem quite as fit to break the pressure of the intestinal contents as to strengthen its hold upon the intestinal wall. In *Trichocephalus* (Fig. 3) the whiplash-like anterior part of the body is actually imbedded in the mucous membrane.

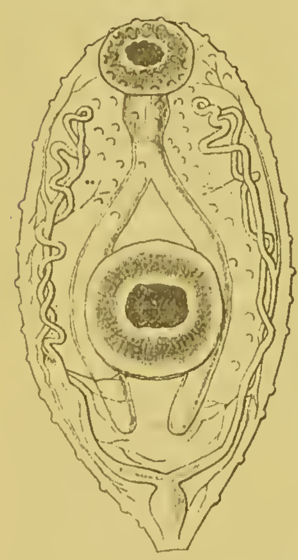


FIG. 1. — *Distomum luteum* (young), with suckers and viscera (after de la Valette).

In this case the form of the body in a certain way makes up for the absence of proper organs of attachment. When these are present we find the greatest differences in their structure and arrangement, which correspond always to the needs and circumstances of the individual parasite. Sometimes, as in the flukes (Fig. 1), muscular suckers are present, which work by atmospheric, or, more correctly speaking, by hydraulic pressure;

sometimes the organs of attachment consist of hooks and claws, which serve to penetrate the underlying tissue or to lay hold of various prominences. In *Tænia solium* (Fig. 4) and other tape-worms these hooks have their basal end sunk within the tissues of the parasite, or else, as in lice (Fig. 2) and the majority of the parasitic Arthropoda, they are situated upon the extremities of the limbs. The various bristles and other prolongations of the outer skin, so commonly met with, may be safely included in the category of organs of attachment. These, by contact with neighbouring parts of the body, not only increase the power of resistance of the parasite, but also prevent it from being displaced in this or that direction, according to their disposition. By the possession of setæ of this kind, the male *Distomum* (*Bilharzia*) *hæmatobium* is able not only to retain its position in the vena cava of man, but also occasionally to advance against the blood stream into the venous plexuses of the urinary bladder and rectum, so as to enable the female, which it drags along with it, to lay its eggs in a convenient place.

Frequently several kinds of organs of attachment are found upon the same parasite; an instance of this is *Tænia solium*, which has

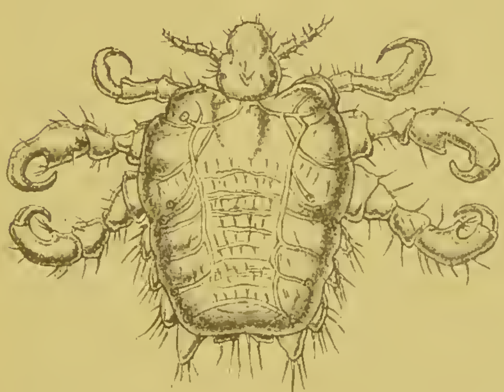


Fig. 2.—*Pediculus* (*Phthirius*) *pubis.*

Fig. 3.—*Trichocephalus dispar*, *in situ.*

just been mentioned. Besides the hooks which are arranged in a circle upon the summit of the head (Fig. 4), there are found a number of suckers, which, together with the hooks, enable it to attach itself so firmly that it is very difficult to remove it from its place. Comparing the four suckers and their position upon the head with the single terminal sucker of the leech and the two suckers of *Distomum* (Fig. 1), we see that the organs of attachment in the parasites offer quite as great differences in their arrangement as in their structure.

It has by this time, I hope, been made clear that the stationary parasite differs much more from ordinary free-living animals, both in the outward form of the body and in its armature, than the temporary parasite. How great the difference really is between these two forms of life, is most distinctly seen in those parasites which are free at one period of their existence; and parasitic at another; the free stage may perhaps be entirely unlike the parasitic, especially in those cases where the conditions of life enjoyed by the animal during its parasitic and free stages differ markedly from each other. The larva of *Gastrus*, which inhabits the stomach of the horse, has all the characters of a stationary parasite; a simple cylindrical body without eyes and sense organs, and, instead of organs of locomotion, organs of attachment in the shape of powerful hooks at both sides of the mouth, and numerous variously sized setæ upon the surface of the body. How different is the form of the adult free-living animal, with its segmented body, eyes, tentacles, legs, and wings! Who would believe that these two creatures were merely stages in the development of the same animal, had not actual observation demonstrated the fact, and shown that the worm-like larva was produced from the eggs laid by the fly.

FIG. 4.—Cephalic end of *Tœnia solium.*

But this striking difference, we cannot doubt, corresponds less to the needs of parasitism as such, than to the differences which usually obtain between a stationary mode of life and a free existence. In this way we can understand the fact, already mentioned, that metamorphoses quite similar to that of *Gastrus* are commonly met with in other insects, where the young are not parasitic, but only live a stationary life like parasites.

Conversely, there are periodic parasites, whose structure, during both stages of their life-history, is quite the same. This is the case with the Gordiaceæ, which pass their young stage in the body-cavity of snails and insects, and afterwards live in water or damp earth without any further ingestion of nutriment. In this instance, however, there is no great difference in the manifestations of life between the free and parasitic stages; in both, the animal leads a stationary existence, and it is only the medium in which it lives that changes.

It has been already pointed out in this chapter that the characters of parasites cannot be said to have the value of specific peculiarities, and this is well shown in certain remarkable cases of parasitism, to

which van Beneden first applied the term "commensalism." Here we have creatures that live within the bodies of larger animals, like parasites, to which they are generally very similar in organization; nevertheless, they are not true parasites, inasmuch as they do not feed upon the juices and tissues of their host, but share its food or live upon the refuse of its body. Although there are several instances of commensalism among the lower aquatic animals, we do not find any in man and the domestic animals, which form the subject of the present treatise, it being supposed, of course, that the conception of the term is not extended to such parasites as live upon the internal excretory products, instead of the living tissues of their host. If it could be definitely proved that certain intestinal worms (such as *Oxyuris curvula* of the horse) really feed upon the undigested food of their host,[1] this statement would need some limitation; but it would at the same time tend to show that commensalism is connected with true parasitism by numerous transitional stages, as we have already seen that the free and parasitic modes of existence are connected.

[1] Dujardin, *Ann. Sci. Nat.*, sér. 3, t. xv., p. 302, 1851.

CHAPTER II.

OCCURRENCE OF PARASITES.

JUST as there is hardly a single creature which is not preyed upon by some carnivorous foe, so it seems probable that every animal gives shelter at one time or another to some parasite. We are even acquainted with cases where the parasite itself is subject to the attacks of other parasites. Many of the parasitic Crustacea, for example, give shelter to mites or thread-worms; the parasitic larva of the ichneumon-fly again is inhabited by other minute parasitic larvæ (Pteromalinæ.) In the case of the Nematode, *Trichosomum crassicauda*, which infests the rat, we find three or four males living parasitically within the uterus of the female.[1] Neither small dimensions nor a concealed mode of life offer the slightest protection against these enemies.

Nevertheless, every animal is by no means equally subject to the attacks of parasites; on the contrary, we find the greatest differences in this respect. In certain animals, the presence of parasites appears to be the rule, since they may be found in great abundance[2] in every individual examined; in certain others hundreds of specimens may be searched without finding a single parasite. On the whole, it may be safely stated that the Vertebrata are far more generally infested by parasites than the Invertebrata, and indeed it was thought for a long time that their occurrence in the latter was a mere accident. Which-

[1] See Vol. II. The recent researches of Bütschli and von Linstow have fully demonstrated this fact. Moreover, there is another free-living worm (*Bonellia*), the male of which in a similar fashion lives within the genital duct of its own female. See Kowalewsky, "Du male planariforme de la Bonellia," *Revue des Sci. Nat.*, pl. iv., 1875 (translated from the Russian); Vejdovsky, *Zeitschr. f. wiss. Zool.*, Bd. xxx., p. 487, 1878; Spengel, *Mittheil. zool. Stat. Neapel*, Bd. i., p. 357 *et seq.*

[2] The snipe, the goose—so long as it lives in meadows—the turbot, have their intestines almost always filled with numerous Helminths, generally Cestodes. How vast is occasionally the number of parasites is shown by certain cases of trichinosis and the Cochin-China diarrhœa. Even the larger intestinal worms are sometimes found in great numbers. Bloch ("Abhandlung von der Erzeugung der Eingeweidewürmer," Berlin, 1782, p. 12) found in a male bustard at least a thousand specimens of *Tænia villosa*, some of which were no less than 4 feet in length. Göze also ("Versuch einer Naturgeschichte der Eingeweidewürmer," 1782, p. 32, note) found the alimentary canal of a parrot so full of Cestodes, 20 ells in length and about the thickness of a straw, "that it (intestine) was almost ready to burst." When the whole mass was placed in water, Göze was astonished

ever opinion may be held—whether we regard the presence of parasites in invertebrates as a necessary preliminary to their sojourn in the body of some vertebrate or not—the fact remains the same. The abundance of parasites within the Vertebrata may be more or less accounted for by the fact that there are normally several, if not a great number of species found in the same host.[1] Thus, for example, man has more than fifty distinct species of parasites, the dog and the ox some two dozen each, the frog perhaps twenty. These are of course not all found in the same place and under similar conditions, but are scattered throughout the various organs and systems. One takes up its abode in the skin, another in the intestines, a third in the connective tissue between the muscles, while others again inhabit the brain or even the eye. No organ or tissue, however remote or concealed, is entirely free from parasites, and it is well known that even the embryo within the body of the mother is occasionally infested by them. What has been already said about the various species of animals, applies equally well to the different organs; some are more liable than others to be inhabited by parasites. The outer skin of the body and the alimentary canal seem on the whole to contain the greatest number, and this because they are more easy of access: in man more than three-fourths of the total number of parasites are found in these two localities.

Frequently the distribution of a given parasite is not confined to a single organ. There are numerous examples, however, of this—*e.g.*, *Trichina spiralis*, when encysted, is found only in striated muscle, the sexually mature Cestodes and *Echinorhynchus* are confined to the intestines, and *Phthirius pubis* only inhabits those parts of the body that are thickly covered with hair; but the converse is almost more general. *Cysticercus cellulosæ*, for instance, infests the intermuscular

at the enormous number, for there were several thousands. This same helminthologist found on another occasion no less than 82 *Ligulæ* in the intestines of a diver, some of which were 6 to 8 ells long and 8 lines broad. Frequently the intestinal worms of an animal belong to several different species. Nathusius (*Archiv f. Naturgesch.*, Jahrg. iii., Bd. i., p. 53, 1837), took from a single black stork 24 specimens of *Filaria labiata* from the lungs, 16 *Syngamus* (*Strongylus*) *trachealis* from the trachea, more than 100 *Spiroptera alata* from the coats of the stomach, several hundred *Holostomum excavatum* from the small intestine, and about a hundred *Distoma ferox* from the intestine, 22 specimens of *Distoma hians* from the œsophagus, 5 *Distoma* (*D. hians* ?) from between the coats of the stomach, and 1 *Distoma echinatum* from the small intestine. This forms quite a helminthological museum; but Krause of Belgrade found even a greater number in a horse two years old—over 500 *Ascaris megalocephala*, 190 *Oxyuris curvula*, several millions of *Strongylus tetracanthus*, 214 *Sclerostomum armatum*, 69 *Tænia perfoliata*, 287 *Filaria papillosa*, and 6 *Cysticerci!* (See van Beneden, "Animal Parasites," p. 91.)

[1] Von Linstow has recently published a useful compilation of the distribution of Helminths, which is the most complete in existence: "Compendium der Helminthologie," Hanover, 1878.

connective tissue, the brain and eye, and many other localities; *Echinococcus* is found in the liver, spleen, kidney, lung, bones, nervous centres, beneath the skin, and, in short, almost everywhere in the human body. Similarly *Filaria papillosa* of the horse is not only found in the peritoneal membrane, but also in the peripheral connective tissue of various parts of the body, and occasionally in the body-cavity, inside the skull and vertebral column, sometimes even in the eye, either in the outer layers, the anterior chamber, or the vitreous body.

The same principle holds good in regard to the relations of a parasite to its host. Some species are limited to a single host; others, again, are parasitic upon several animals, not merely at different periods of their existence—passing their youth in the body of one animal, and attaining their maturity in that of another—but also during the same phase of development. In the first group may be reckoned among human parasites, *Pediculus capitis*, *Bothriocephalus latus*, and *Oxyuris vermicularis*; also *Tænia crassicollis* of the cat, and *Echinorhynchus gigas* of the pig. To the second group belong by far the greater number of parasites, such as *Strongylus gigas*, which is found in many Carnivora—in the genera *Canis*, *Mustela*, *Nasua*, &c., in the horse, the ox, and in man; *Trichina spiralis*, which not only infests man, the pig, and the rat, but also the hedgehog, fox, martin, dog, cat, rabbit, ox, and horse, and may be transplanted even to birds. *Distomum hepaticum* has also a very wide distribution among warm-blooded animals, being found in most Ruminantia, Perissodactyla, Pachydermata, and Rodentia, and also in the kangaroo, in man, &c. Although it is a general rule that a parasite infests several distinct animals, it is equally true that the distribution of parasites is governed by certain laws. The examples just cited show this clearly. The various animals which are infested by one and the same parasite are always more or less closely related to each other. It is most usual to find that the related species of a given genus, or the genera of a given family, harbour the same parasites; there are, indeed, only very few exceptions to this rule, such as *Trichina spiralis*. But even in these rare cases a certain relation can be observed between the different hosts; and a parasite which in the same stage of its existence infests sometimes a mammal or a fish, sometimes a mollusc, is quite unknown. This fact becomes more evident when we examine not merely the number of hosts in which a given parasite is met with, but also the statistics of the distribution of parasites, and discover the number of times which it is found in each host; for instance, in other words, *Distomum hepaticum* is only rarely found in man, the kangaroo, and rodents, while it is commonly met with in ruminants, especially in the sheep. The same holds good

in the case of *Strongylus gigas*, which is far more abundant in carnivorous than in herbivorous animals, while it has only been met with a few times in man and other hosts. By the help of the statistical method it is easy to find out what are the animals most frequented by a given parasite, and the results obtained show that the several hosts are always more or less allied to the one in which the parasite is most commonly found. The causes of this are no doubt various, and partly of a kind which will be discussed later on, when we come to examine into the life-histories, origin, and migrations of parasites; but for the present it may be remarked that these causes are to be looked for partly in the hosts themselves (in their distribution, habits, manner of locomotion, and their food), partly also in the nature, condition, and needs of the parasites.

The factors which we are considering now are nearly the same as those which govern the relations between carnivorous and herbivorous animals, inasmuch as they concern not merely the actual carnivorous instinct, but also the choice of the prey. We need not be surprised, therefore, that a carnivorous mode of life, as has been already pointed out, is unmistakeably related to a parasitic mode of life.

A very cursory examination of the conditions of life proves that we are right in regarding the distribution of parasites as greatly dependent upon the nature of the host as well as of the parasite itself. It is clear, for instance, that a parasite with lungs and other organs that need a direct contact with the air, can only exist in those creatures whose structure and mode of life render this possible, and only in those parts of the body to which the air has free access. Thus, all parasitic air-breathing insects (including Arachnida) are, without exception, confined to terrestrial or amphibious animals, and generally to their external skin. The walrus, for example, harbours a *Pediculus* of considerable size. On the other hand, the external parasites of aquatic animals generally belong to the Crustacea or some group which breathes by means of gills, and therefore needs direct contact with water. Worms breathe by means of the skin, and hence the parasitic members of this group—the so-called Helminths—are sometimes found as ectoparasites upon aquatic animals, while they are usually met with only in the interior of terrestrial animals, in organs where they are bathed in the oxygenating fluids of their host. Parasitic worms are also found in similar situations within the bodies of aquatic animals, but this is quite intelligible, inasmuch as they are of all parasites the most widely diffused; in fact, internal parasites, or "Entozoa," as they are usually termed, are mainly worms.

With this wide distribution may be coupled the fact that parasitic worms are numerically far more abundant than parasitic Arthropoda;

the latter, moreover, live in comparatively similar circumstances, while the conditions of entoparasitism are most varied.

It must not be forgotten, however, that there are a few entoparasitic Arthropoda belonging to the Insecta and Arachnida. The most striking example is furnished by the Pentastomida (Fig. 5), which, during the early stages of their existence, inhabit the internal organs of both terrestrial and aquatic animals, and on this account were included by the earlier helminthologists among the Helminths proper. A closer investigation has shown that this classification, though hardly to be wondered at, is erroneous ; the Pentastomida are undoubtedly to be referred to the Arachnida, but they differ from them by the entire absence of lungs, and in this respect approach the intestinal worms. Many mites also (Fig. 6) possess no respiratory organs, and agree with the Pentastomida in breathing by means of the skin ; this is facilitated by their small size, which implies a relatively large surface, and by the fact that they are usually to be found in damp situations, sometimes imbedded in the epidermis (*Sarcoptes*), almost entoparasitic, sometimes upon the hairy portions of the skin (*Dermatodectes*, &c.). But these instances must not be considered as proving that all entoparasitic Arachnida and

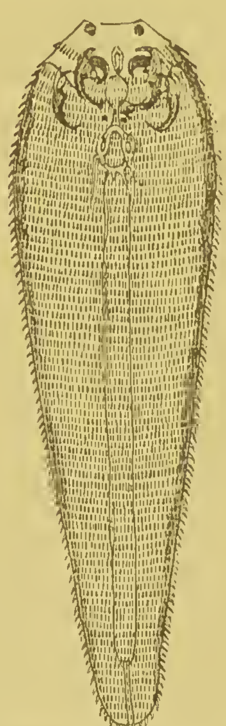


FIG. 5.—*Pentastomum denticulatum* from the liver of man.

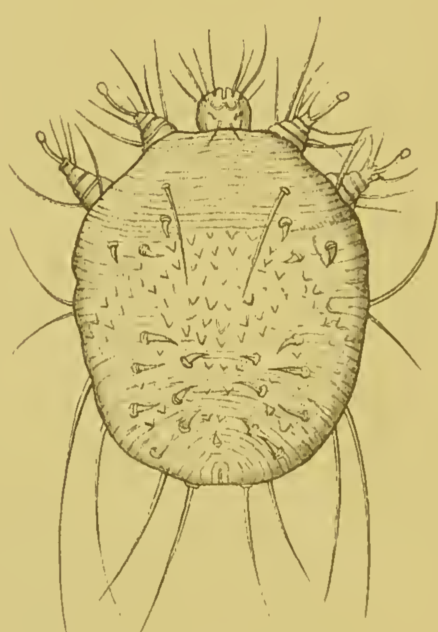


FIG. 6.—*Sarcoptes scabiei.*

Insecta differ from their immediate allies by the absence of respiratory organs. On the contrary, the majority possess the normal tube-like

lungs (the so-called "tracheæ"), and need therefore a direct contact with the air. To understand this properly, we must remember that contact with the air is by no means confined to the outer surface of the body; many of the internal organs are either continuously or occasionally in communication with the outer air; and all these organs, in spite of their position in the interior of the body, are occasionally inhabited by air-breathing parasites.

We often find the larvæ of flies within the nose and frontal sinuses of mammals, especially the sheep (*Oestrus ovis*); sometimes, as has been recently reported from Guiana, in man himself (*Lucilia hominivora* and *Sarcophaga Wohlfarti*, both belonging to the Muscidæ); the larvæ of flies (*Musca vomitoria, Anthomyia canicularis*, Figs. 7 and 8) are also sometimes found in the intestine, especially in its interior portion, where air frequently enters along with the food; indeed the larvæ of *Gastrus equi* are almost constantly found in the horse in this situation. Other air-breathing parasites live below the skin of mammals (as the larvæ of *Oestrus* and the chigoe), and dwell not in enclosed spaces, but in passages open to the air; in these cases the apertures of the respiratory organs of the parasite are generally turned towards the exterior, to permit of a free exchange of air. Similarly, in parasitic larvæ within the body-cavities of insects, the hinder

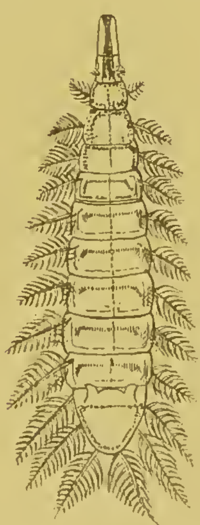


FIG. 7.—Larva of *Anthomyia canicularis* from the intestine of man.

FIG. 8.—Larvæ of *Musca vomitoria*.

portion of the body with its tracheal opening is usually (as in the chigoe) protruded through the outer skin of its host, or is in communication with the tracheæ of the latter. The occasional presence of dipterous larvæ in wounds, abscesses, even in the vagina, and under the præputium and eyelids, is well known, and is easy to understand,

after what has just been said, since these parts of the body, being on the outside, are precisely the situations most convenient to parasites of this kind. Where respiration is impossible, there can evidently be no air-breathing parasites, and all notices of fly-larvæ discovered in such situations, as for example, within the internal urinary passages, are to be regarded as mere fables. The absolute need of access of air, which parasites of this description have, can be easily proved by experiment. I have frequently introduced the larvæ of *Musca vomitoria* at all stages, even as eggs, into the body-cavity of dogs and rabbits through apertures in the abdomen, but never in a single instance observed any further development take place; in most cases they died very shortly.

From the foregoing remarks, it follows that parasites may be divided into two groups—*ectoparasites* (Epizoa, external parasites) and *entoparasites* (Entozoa, internal parasites). I am well aware that in certain cases this distinction is not more easy to make than that between internal and external organs, and that the two groups by no means include all the peculiar forms of parasitic life; but it is on the whole convenient to retain it, to express the general conditions of parasitism with which we are for the present concerned.

The ectoparasite inhabits the most readily accessible organs of the body of its host, which it frequently abandons at pleasure. The group which we have already alluded to as temporary parasites are, with a few exceptions, ectoparasitic. In the same way, the semi-stationary parasites are usually found upon the outer skin, where the least hindrance is offered to their movements, while the entirely stationary parasites are more commonly met with in the internal organs. It follows, therefore, that ectoparasites can generally be recognised as such by their outward form, especially by the structure of their organs of locomotion.

In certain ectoparasites, which have but a slight locomotive capacity, there are usually found, either upon the organs of locomotion (Fig. 2), or (as in ectoparasitic worms) in their stead, powerful organs of attachment, which are generally more strongly developed than in the Entozoa. These structures enable them to cling very firmly, and prevent them from being detached by the movements of the animal upon which they live. The great differences that exist between these organs in different parasites are greatly dependent upon the mode of life of their host and the structure of its outer skin.

With regard to respiration, the ectoparasite, as has been already remarked, depends upon its host, and shares with it the same conditions of life. It usually possesses special organs of respiration, especially when living upon terrestrial animals, and being, therefore, in direct

contact with the air. The possession of these organs is an almost exclusive attribute of ectoparasites; for the Entozoa belong, with a few exceptions, to the group of worms which breathe by means of the skin. The Entozoa, besides having no special respiratory organs, are also without pigment, the skin being whitish and transparent: in this they agree with many other creatures, which, like themselves, are removed from the influence of light. The ectoparasites, on the other hand, especially the temporary parasites, agree in these respects with free-living animals.

The modifications undergone by parasites, to adapt them to the various conditions, are also to be noticed in the structure of the mouth organs.

Parasites upon the outer skin, of the higher Vertebrata at any rate, can obtain no other nutriment than a more or less firm horny substance belonging partly to the epidermis and partly to the structures that originate from it; it is needful, therefore, that they should possess some apparatus strong enough to gnaw through these hard tissues, and this we find, in the form of powerful jaws, in many lice, and especially in the Mallophaga. In the same way, parasites that feed upon the blood of their host must be able to bore through its epidermis, in order to reach their food and then suck it up. In these cases we find either mandibles, surrounded by a circular lip that plays the part of a sucker, as in the leech (Fig. 9), or a boring apparatus, as in the common lice, bugs, fleas, and mosquitoes, which has the advantage of working rapidly, and is therefore specially adapted to these parasites which only visit their host for a short time.

Fig. 9.—Cephalic end of *Hirudo medicinalis*, with the three mandibles at the base of the oral cup.

The necessity of a special mouth apparatus can only be dispensed with in those ectoparasites that live upon an animal which has a soft skin, as is generally the case in aquatic animals. The parasite, then, is provided with some contrivance that enables it to suck; generally a pharynx, or some muscular apparatus which allows of an alternate widening and narrowing of the mouth cavity, or which under other circumstances may cause merely a peristaltic action.

The Entozoa generally possess some apparatus of this kind in contradistinction to the ectoparasites, and are but rarely provided with jaws like the latter, except in a few cases, such as *Dochmius duodenalis* (Fig. 10), which, although parasitic in the intestine, lives upon the blood of its host, and not upon the epithelial lining or contents of the intestine; and is in this respect, therefore, analogous to an ectoparasite. Since most entoparasites are entirely nourished by

the fluid or semi-fluid substances which surround them, the presence of the above-mentioned sucking organs is quite intelligible; they are

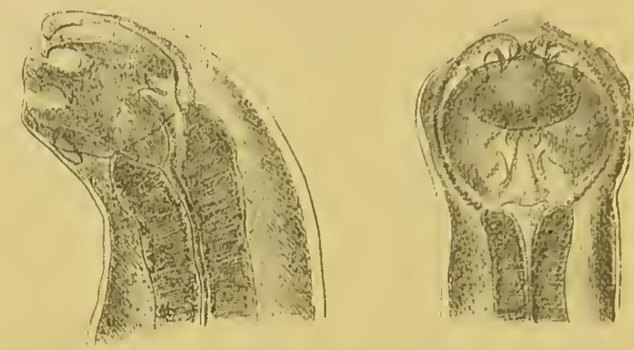


Fig. 10.—Cephalic extremity of *Dochmius duodenalis*; profile and front view.

Fig. 11.—A male *Echinorhynchus angustatus*. (The internal organs consist of the sheath of the proboscis, with retractor muscle, lemniscus, and sexual organs. An intestine is wanting.)

not, however, absolutely necessary. Many Entozoa have no muscular pharynx, and are sometimes even entirely destitute of an alimentary canal, and must absorb their food through the surface of the body, after the fashion of a plant, without the action of any further process. The Cestodes and *Echinorhynchus* belong to this class, and their outer skin possesses the requisite permeability to a high degree, as may be easily proved by placing the animals in water, when they swell up rapidly. Of course, it is only substances dissolved in fluids that can find their way into the interior of the bodies of these parasites; but they usually live in situations where they are surrounded by nutritive fluids to such an extent that they may be regarded as almost swimming in them.[1] In all probability, this way of taking in nutriment by endosmosis is not confined to the anenterous forms, but exists generally among Entozoa, though it undergoes various modifications in correspondence with the various differences of structure in the outer covering of the body. From this point of view, the Entozoa may be

[1] In the Rhizocephalida (*Sacculina*, &c.) we have recently discovered a group of ectoparasitic Crustacea that have no alimentary canal. They obtain their food like plants, by a number of branched prolongations, which pass through the body of their host and ramify in its intestine. They are found generally on the ventral surface of the abdomen of crabs. With respect to these interesting parasites see especially Kossman, "Suctoria and Lepadidæ:" Heidelberger Habilitationsschrift, 1873.

regarded as really an integral part of their host; they are quite comparable, in respect of the way in which they are nourished (and breathe), with a cell, or an embryo. They manufacture their food in a precisely similar manner out of the juices surrounding them, which, by chemical change, minister to the conditions of their life and growth and remove their waste products.

The presence of a mouth and intestine is not, however, rendered superfluous by the universality of this method of taking in food by endosmosis; they not only enable their possessor to feed upon other semi-fluid or solid matters,[1] but also serve the purpose of increasing the absorbent surface in cases where solid food-matter is not utilised.

All that has been said hitherto refers to Entozoa that live in absolute contact with the tissues of their host, which is generally, but by no means always, the case. In the parenchymatous organs, a membranous cyst usually surrounds and isolates the parasite, with which it has no direct connection. It is a part of the infected organ, a hypertrophy of the surrounding connective tissue, which gradually encloses the parasite completely; a similar cyst is, indeed, formed round other foreign bodies introduced into the organ, and becomes very like a serous membrane, owing to the development on its free surface of a more or less thick epithelial layer (endothelium).—(Figs. 12-14.)

Fig. 12.—*Cysticercus pisiformis* (young).

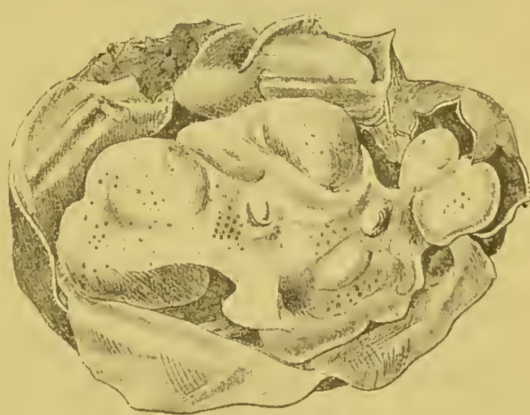


Fig. 13.—*Echinococcus.*

This capsule is regarded, and no doubt rightly, as an organ for the protection of the infected part; but, at the same time, it must not be

[1] How great an influence the quality and abundance of the food has upon the parasite is strikingly shown in the case of *Polystomum integerrimum.* This Trematode usually inhabits for a short time the gill cavity of tadpoles, and then wanders into the bladder, where it becomes sexually mature in about four years; if it remain longer in the branchial cavity, it only takes twenty-seven days to reach sexual maturity. It is not merely the

forgotten that it is of no less importance for the nourishment of the contained parasite. The blood-vessels which traverse the capsule, and occasionally form a definite system with afferent and efferent vessels, supply fluid nutriment, which is absorbed by the parasite through its mouth or skin, and which varies in quality according to the structure of the capsule. On the whole, it appears that worms encysted in parenchymatous organs do not receive a great deal of nutriment, since they often remain unchanged for years, and even longer periods, while the same worms, under other circumstances—by migration to the intestine, for instance—rapidly grow and undergo further development. This capsule is most conspicuous in the so-called bladder-worms, especially in those which grow to a large size, and inhabit organs rich in connective tissue. In these cases (*Echinococcus*) the cyst becomes occasionally several millimetres in thickness, and so firm that it can be easily removed without injury from the surrounding parenchyma.—(Fig. 13.) Traces of a cyst are, however, found in all worms which remain for any length of time in parenchymatous organs, even when they only attain to a small size. In these cases, however, the hypertrophy of the connective tissue, caused apparently by the irritation set up through the presence of the parasite, can hardly be recognised as a continuous (independent) cyst.

FIG. 14.—*Sclerostomum tetracanthum*, encysted.

Many worms which inhabit parenchymatous organs secrete on the inner surface of their connective tissue capsule a cuticular cyst, which is, of course, sharply marked off from the former by its histological structure.

It appears in the form of a homogeneous membrane, consisting of concentric layers; it resists the action of alkalies, and belongs, apparently, to the chitinous formation so generally met with in the lower animals.[1] This chitinous cyst is most usually found in the Trematodes, but is not wholly absent in the other groups, being found, for example, in *Tetrarhynchus*, which lives in fishes, and even in the muscle-*Trichina* (Fig. 15), the cysts of which are nothing

rapidity of development which characterises these individuals; they differ also from the common form in a number of anatomical peculiarities, notably by the absence of copulatory organs. See the interesting observations of Zeller, *Zeitschr. f. wiss. Zool.*, Bd. xxvii., p. 238 *et seq.*, 1876.

[1] Waldenburg is of opinion that this chitinous capsule is in some cases formed by the host. See *Archiv f. pathol. Anat. u. Physiol.*, Bd. xxiv., p. 157, 1862.

else than a calcareous excretory product of the worm itself, on the outside of which there lies the connective tissue capsule.

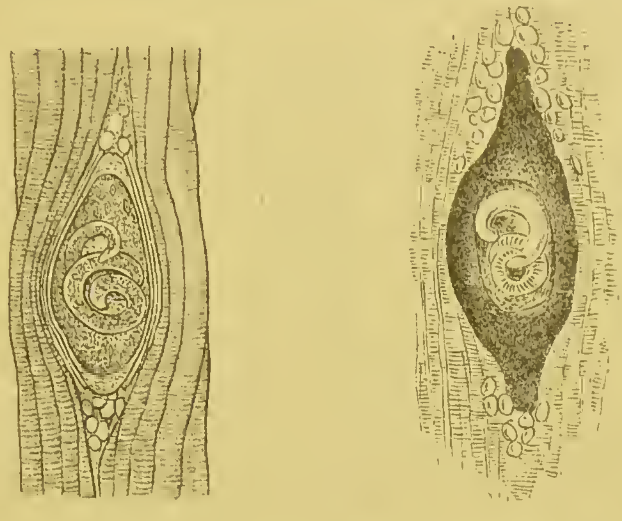


FIG. 15.—*Trichina*-capsule, with connective tissue covering (*in situ*), in B calcified.

CHAPTER III.

THE THEORY OF THE ORIGIN OF PARASITES REGARDED HISTORICALLY.

Were the parasites infesting animals confined to those which are temporary and external, their origin and descent would present no difficulties to the observer. But numerous forms are found deep in the interior of living bodies, in the brain, kidneys, and other apparently inaccessible organs. It is very surprising, when we expect to meet with only the blood, nerves, and other constituent tissues of the body, to find independent living animals, frequently of large size, which have left no trace to show how they reached their dwelling-place, and, indeed, are often incapable of moving about. Under these circumstances, we can easily understand that the presence of parasites has an unusual interest, and that their origin was one of the subjects most eagerly investigated by biologists. The importance of parasites from a medical as well as from a zoological point of view, caused both physicians and naturalists to examine more closely into these facts, which appeared as mysterious and incomprehensible as the origin of life itself.

In its most general aspect, the question of the origin of internal parasites can be answered only in two ways; either they originate in the tissues in which they are found, or else reach them from the external world. In the former case, they must be spontaneously generated; in the latter they may, after the ordinary method, be developed from fertilised ova. Indeed, all the conjectures and hypotheses as to the origin of Entozoa brought forward in former centuries can be reduced to these two theories, though the greatest diversities, depending partly upon the views current at the time, and partly upon individual opinions, are to be seen in the way in which these theories were stated. Where facts are silent, there imagination is the more eloquent; and it is only in our time that a definite solution has been put forward as to the origin of parasites, which rests at the same time time on a firm basis of fact.

As long as it was believed that a "*generatio æquivoca*," or "spontaneous generation," as it is usually termed, was a phenomenon commonly met with among the lower animals, the origin

of intestinal worms could be readily explained. They were a striking instance of spontaneous generation, the existence of which was already contended for in by far the greater number of the lower animals. At most, the discussion related to the particular formative material out of which the newly created organism was made, and whether it was first an egg or appeared at once as an adult. Sometimes it was the blood and juices of the body, at another time the excretions of the alimentary canal or the digested food, that was supposed to be the formative substratum of the spontaneous generation; and it was disputed as to whether fermentation or putrefaction, or a special organizing principle, gave the first impulse to its creation.

These were the opinions held by the Ancients, and throughout the Middle Ages, so fruitless in scientific research. It was not until the seventeenth century that the theory of the generation of animals was reformed, and at the same time an entire revolution in the opinions as to the origin of Entozoa inaugurated.

The researches of Swammerdam and Redi had the most profound influence, and entirely contradicted the earlier theories, that sexual generation was confined to the higher animals. They showed that sexual generation, precisely similar to that of birds, mammals, &c., was found in many of the lower animals; such as the insect, whose development and metamorphosis were for the first time worked out by these two naturalists; not even the parasitic insects being neglected.

Redi clearly proved by his researches and experiments that the maggots, which had been formerly considered as independent organisms (Helcophagi), were in reality the larvæ of flies, and that they were only developed when the fully formed insects were allowed access to deposit their eggs.[1] Swammerdam, in the same way, showed that lice were developed from eggs;[2] he was also well aware (according to the communications of the painter O. Marsilius) that the parasitic larvæ in caterpillars were the offspring of insects that were in the habit of laying their eggs beneath the skin of these same caterpillars.[3]

With respect to the intestinal worms, neither of these observers brought any direct evidence against the generally received opinions. Certainly not Redi, who put forward a view as to their origin, which differed only by a somewhat metaphysical tinge from the widely spread theory of *generatio æquivoca*. Swammerdam expressly guards against any application of his experiments concerning the development of insects to the Entozoa. It appears, indeed, as if he

[1] Redi, "Esperienze intorno agl' insetti," t. i. p. 23: Venezia, 1712.
[2] "Bibel der Natur" (aus dem Holländischen übersetzt), p. 37, 1752.
[3] *Ibid.*, p. 281.

chiefly wished to prevent it from being thought that intestinal worms were derived from insects and other free-living animals; nevertheless, he does not deny the theory that they originate from the eggs of species "that have already existed in the intestines of other animals."

But in spite of the anathemas which Swammerdam hurled against the theory of the heterogeneous development of the Entozoa, this theory shortly after was very generally accepted.

While, on the one hand, the existence of sexual generation in animals was being shown to be more and more universal, and became more definite, the microscope, newly applied to scientific researches, revealed a whole host of minute creatures, which, in spite of their wide distribution, had hitherto escaped attention on account of their small size. Animalcules were found in drinking water and in food, in the earth, and were supposed to exist even in the air: was it not natural that under the influence of these discoveries the theory of the heterogeny of Entozoa fell upon a fruitful soil? The introduction of these creatures into the human body appeared almost inevitably to lead to the conclusion that, when acted upon by the warmth and abundant nutriment in the body, they increased in size and became veritable Entozoa. It is not surprising, therefore, that men like Boerhaave [1] and Hoffmann [2] traced back the Cestodes and Nematodes to animals which, when existing in the free state, were totally different in appearance. The creatures that were supposed to be the progenitors of the Entozoa were by no means the Infusoria alone, but sometimes other larger creatures, such as free-living worms, and specially such worms as possessed a superficial resemblance to the Entozoa. Although a theory of this kind appears to us now entirely unscientific, we must not forget that at that time discoveries in the metamorphosis of animals were too recent and incomplete to allow of a just appreciation of the law of stability of species and their cyclical development.

The actual nature of parasitic worms did not long remain unknown. Not only did naturalists gradually come to see that the occasional change of free-living animals into Entozoa was in entire contradiction to the common phenomena of generation and development, but they learnt to recognise the Entozoa as sexual animals, whose organic structure marked them out as representatives of special classes of animals.

At the same time, however, it appeared that these creatures did not exist exclusively as Entozoa, but that they were also capable of a free existence. By a careful and systematic examination of our rivers and streams, a number of animal forms were discovered that appeared

[1] "Aphorism.," 1360. [2] "Opera," t. iii., p. 490.

strikingly like the Entozoa, and sometimes were even actual Entozoa. Of special import was the discovery of a tape-worm in fresh water by Linné,[1] and subsequently by several other naturalists in different places. We now know that this tape-worm (*Bothriocephalus* v. *Schistocephalus solidus*) inhabits originally the body-cavity of the stickleback, which it abandons at a certain stage of its development, and passes some time in the water, being finally swallowed by a water-fowl.[2] Linné, however, did not know these facts, and regarded the worm without hesitation as a young and incomplete specimen of the large human tape-worm (*Bothriocephalus latus*), and believed, therefore, that this worm was conveyed into the body from the exterior, where it already existed fully formed, in water. Moreover, this assertion was not confined to the tape-worm; Linné believed that he had also discovered the liver-fluke of the sheep and the *Oxyuris* of man leading a free existence; but there is no doubt that he mistook a Planarian for the former and one of the free-living Anguillulidæ for the latter.[3]

However small the evidence was, it appeared sufficient to establish this idea, which was believed in by many naturalists after Linné, chiefly because the facts known at that time about the Entozoa, as well as other parasites which we shall have to consider, were extremely fragmentary. To illustrate the small degree in which helminthology was known at that time, it may be mentioned that in spite of the vast numbers of existing Entozoa, not more than a dozen—and these almost entirely human parasites—had been described.

Soon after this commenced a new era in helminthology. The knowledge of intestinal worms, which was till then chiefly of medical interest and cultivated by medical men, gradually began, under the influence of the Linnæan school, to attract the attention of zoologists. Men of high ability and wide knowledge, like Pallas, O. F. Müller, and others, bestowed upon this science their special attention, and increased our knowledge of parasites in all directions. But every new parasite and new host rendered less probable the idea of Linné that these animals lived sometimes freely and sometimes as parasites.

The number of known Helminths soon became very considerable, but all attempts to find them living in a free state were in vain,

[1] "Amœnit. Acad.," t. ii., Erlangæ, 1787, p. 93.

[2] Steenstrup, *Overs. K. dansk. Videnskab. Selsk. Forhandl.*, p. 166, 1857: *Zeitschr. d. gesammt. Naturwiss.*, Bd. xiv., p. 475, 1859. In a similar manner *Ligula* frequently leaves the body of the fish in which it is parasitic at a certain stage of its development, and leads a free life, see Bloch, "Abhandl. von der Erzeugung der Eingeweidewürmer," p. 2, 1782.

[3] "Systema Naturæ," ed. x., t. i., p. 648. *Fasciola hepatica*, "habitat in aquis dulcibus ad radices lapidum, inque hepate pecorum." *Ascaris vermicularis*, "habitat in paludibus, in radicibus plantarum putrescentibus, in intestinis puerorum et equi."

and yet no locality was left unsearched; and gradually arose the conviction that the statements of the free existence of intestinal worms were, in the majority of cases, based upon a confusion of these worms with others closely resembling them, and that in those instances (*e.g.*, the tape-worm found by Linné), where an intestinal worm appeared to have been found living free, the discovery could not be interpreted in the sense Linné supposed.

A new theory took the place of the old one. Basing his opinion upon the facts that the eggs of intestinal worms are expelled with the fæces of the animal in which they live, sometimes enclosed in a portion of the body of their parent, as in the Cestodes, and that they remain unaltered for a long time in water, Pallas [1] put forward the view that Entozoa agree with other animals in originating from eggs which can be carried from one animal to another. "It cannot be doubted," he says, "that the eggs of the Entozoa are scattered abroad and undergo various changes without loss of vitality, and that immediately they reach the body of a suitable animal, through the medium of its food or drink, they grow into worms." Of course the eggs in this way could only reach the alimentary canal; but since the Entozoa were found not only here, but also in other organs—liver, muscles, brain—the only possible explanation was that the eggs entered the blood-vessels from the intestine, and were carried "by the blood stream" to those various and apparently inaccessible organs. By the help of the blood-vessels, Pallas believed that the eggs occasionally reached the body of the embryo before it was born; in this way intestinal worms could also be inherited by one host from another.

This was not, however, the first time that the theory of the "inheritance of Entozoa" had been propounded. Even in the days of Leeuwenhoek, Vallisnieri [2] had endeavoured to explain the presence of Entozoa by supposing them to be transmitted from parents to children; and this hypothesis had many supporters, including certain of his illustrious contemporaries (Hartsoeker, Andry, &c.) and numerous later helminthologists, as O. F. Müller,[3] Bloch,[4] and Göze.[5] On this hypothesis, the intestinal worms must have originated in the way just indicated; they must have been innate, or at least have been received by direct transference (for instance by kissing or being suckled). Otherwise, a subsequent

[1] *Neue nord. Beiträge*, Bd. i., p. 43, Bd. ii., p. 80.

[2] "Opere fisico med.," t. i., 1733.

[3] *Naturforscher*, Bd. xiv., 195, 1780. *Neues Hamburger Magazin*, Bd. xx., 1784.

[4] "Abhandlung von der Erzeugung der Eingeweidewürmer:" Berlin, p. 37, 1782.

[5] "Versuch einer Naturgeschichte der Eingeweidewürmer:" Blankenburg, p. 4, &c. 1782.

migration was disproved. The eggs which are extruded with the fæces are, as far as the intestinal worm is concerned, lost,—though they may serve as food for other animals (Göze). It was certainly astonishing that by far the greater number of eggs should incur this fate, but even this fact was brought into accordance with the theory. It was asserted that the intestinal worms, which could not, like other animals, deposit their eggs in a chosen place, must leave it to chance whether they passed into the blood-vessels or not; and furthermore, that the probability of such a haphazard transference was far less than that they should be extruded from the body before it could take place (Bloch).

That this view, under the influence of that theory of evolution which was then dominant, degenerated into wonderful subtleties and refinements in many of its supporters, must not be considered as due to the theory itself;[1] but in other respects it shows so many weak points, that it seems hardly necessary to refute it by calling to mind the various worm-epidemics (sheep-cough, liver rot, &c.), or the *Cœnurus* that almost invariably kills its host, and generally before it arrives at sexual maturity. The influences, however, which led to this opinion are not difficult to understand. On the one hand was the undeniable fact of the sexuality of the Entozoa and their striking fertility; on the other, the difficulty, apparently even impossibility, of tracing the origin of these animals to the eggs extruded with the fæces. The idea of hereditary transmission seemed to afford a way out of this dilemma, and appeared all the more feasible, seeing that many observers stated that they had found Entozoa not only in the young of animals, but even in the embryo within the body of the mother. Whether the cases here alleged were reliable or not,[2] is a matter of indifference to us, but it is surprising, and hardly agrees with this theory of inheritance, that these cases were extremely few in number. It was, accordingly, hardly unjustifiable in Pallas to use not only the directly transmitted eggs, but also those evacuated from the body, to explain entoparasitism. He did not succeed, however, in proving his opinions by direct experiment, any more than his illustrious contemporary, van Doeveren,[3] who also endeavoured to explain the distribution of Entozoa by the theory of the transference of similar germs, but we must not forget to pay our acknowledgment to the clear and accurate perceptions of this great naturalist. *Entozoa do actually originate*, as we now

[1] According to Eberhard's "Neue Apologie des Socrates" (Th. ii., p. 333), the parasites were present as eggs during the age of innocence, but were hatched after the Fall.

[2] For a list of these cases see Bloch, *loc. cit.*, p. 38; also Davaine, "Traité des Entozoaires," 2me ed., p. 11: Paris, 1877.

[3] "Abhandlung von den Würmern in den Gedärmen des menschlichen Körpers," p. 106: Leipzig, 1776.

know well, *from transmitted germs, and only in consequence of a process of generation,* similar to that which exists in the rest of the animal kingdom.

In spite of the accordance between our present knowledge and the theories of van Doeveren and Pallas, the one is not the direct outcome of the other. The path of science strays now on one side, now on another side of the direct line of truth, and we ought not, therefore, to be surprised that the theory just quoted was pushed out of the way by other theories before it had time to take root.

With Pallas, Bloch, and Göze began a long list of helminthologists, of whom the most eminent were Rudolphi and Bremser. Thousands of animals were examined for their parasites, and with such success, that the number of the known Entozoa was soon estimated at many hundreds. As the material got larger, the science of helminthology became gradually more and more separated from zoology, and treated as a distinct specialty. This distinction had its evil effects. It caused helminthology to become a mere descriptive enumeration, hardly at all concerned with the life-histories and development of the animals so carefully registered. This one-sided way of looking at parasites was hardly suitable for solving the questions concerning their origin by careful and unprejudiced experiment. That all previous attempts to explain the presence of these remarkable creatures by the theory of their introduction into the body of their host from without were more or less conspicuously faulty was never at any time doubtful, and perhaps least of all at the present moment. Instead of increasing the number of known facts by the empirical method, and getting, where possible, fresh support on which to base some theory, which might, although not completely proved, furnish numerous and weighty arguments for induction, helminthologists were content to point out the insufficiency of earlier investigations, and return again to the almost forgotten theory of spontaneous generation,[1] which was at any rate a convenient and simple method of cutting the knot.

Those were the times when the all-powerful "vital force," governed the organism. And it seemed an easy thing for this "vitality" to organize a mass of mucus, a villus of the intestine, or a fragment of connective tissue, perhaps by an intensified abnormal process of development, into a bladder-worm instead of a simple hydatid. The structure of the Entozoa was regarded as comparatively simple, and it appeared, therefore, that from this point of view no great difficulties stood in

[1] See specially the excellent work of Bremser, "Lebende Würmer im lebenden Menschen," pp. 1-16 : Wien, 1819.

the way of such a theory. The microscope had been for some time laid aside as a not very trustworthy agent, and a simple lens, or the naked eye alone, was sufficient to watch the process of spontaneous generation.[1] When this had once taken place, it was supposed that the Entozoa increased by sexual generation, or else to what purpose had they been provided with generative organs? The significance of this sexual generation had been kept in the background by the prevailing opinion of spontaneous generation. The majority of the eggs were extruded without being further developed, for, if not, the extraordinary fertility of these creatures would entirely fill their host with their progeny. The supporters of this view, from being well-known authorities in their subject, had such weight, that they readily crushed the evidence advanced against their theory by other observers. This misfortune was partly the fault of their opponents, generally men like Brera,[2] who, in spite of all other qualifications, was ignorant of the necessary details of the subject. As long as Rudolphi's teaching was followed, and the theory of vitality was generally accepted, this view just stated of the origin of the Entozoa was the only one that obtained credence; and it appeared to be strengthened by the discovery of a continually increasing number of bladder-worms and encysted Helminths which were entirely destitute of organs of generation, and were unable, therefore, to propagate themselves by the sexual method. Except by a theory of spontaneous generation, the existence of these worms appeared inexplicable. And yet this appearance was deceptive—so much so, that it is by the help of these very sexless worms that we are now able to show the error of Rudolphi's theory. The general acceptance of this erroneous theory was not, however, overthrown at a single blow. It was necessary to bring forward numerous facts in order to shatter the belief in spontaneous generation, and set a more credible theory in its place; but these facts would not have been recognised for a long period, had not a change in the direction and method of biological study given a fresh impulse to helminthology.

The majority of these fundamental facts were discovered by means of the microscope, which v. Baer, Purkinje, Ehrenberg, and others had again used for scientific investigation, whereby the most brilliant results had already been obtained in other regions of zoology. The first discoveries made by the microscope in helminthology had a most important bearing on the origin of the intestinal worms.

In the year 1831 Mehlis made the remarkable discovery that the

[1] Bremser, *loc. cit.*, p. 65. Rudolphi, "Entozoorum Hist. Nat.," vol. i., p. 811, 1808.
[2] "Medicinisch-praktische Vorlesungen über Eingeweidewürmer,' p. 47 *et. seq.*, 1803.

eggs of certain Distomidæ contained an embryo (Fig. 16) which in shape and ciliation resembled an Infusorian; it was occasionally provided with an eye-speck, and after being hatched swam about like a Infusorian.[1] What a blow was this simple discovery to the earlier theories as to the fate of the eggs of Entozoa. It had certainly been known from the time of Göze that there were a few viviparous Entozoa, but these were in every case thread-worms, whose young so closely resembled the parent form, that they might easily be supposed to attain to their full development without any migration or further change. In the case discovered by Mehlis, however, the eggs had been laid, and the embryos, entirely unlike their parent, seemed, from their eye-specks and coating of cilia, fitted for a free existence. We recall at once the opinions expressed by Leeuwenhoek and Pallas, and it is quite intelligible that von Nordmann, who first confirmed the observation of Mehlis, remarked that these parasites, instead of originating by spontaneous generation, "always sojourn during their first life-period in water, and subsequently enter the body of some animal, where they lose their eye-specks and become sexually mature."[2] Von Nordmann certainly acknowledges that this sounds "fabulous" in comparison with the generally accepted theory, but, after further reflection, he insisted upon it, since he found in the gut of a Neuropterous larva, three-quarters of a line long, a species of Nematode with a conspicuous red eye, which was found also living independently in water.

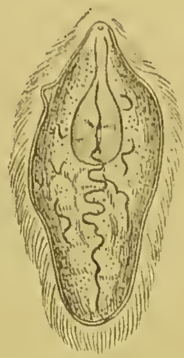


Fig. 16.—Ciliated embryo of *Monostomum capitellatum.*

Soon afterwards von Siebold[3] added to these observations the remarkable fact that the ciliated embryo of *Monostomum mutabile* (Fig. 17), a parasite of water-birds, sheltered within its body another creature (a "necessary parasite," as it is termed), which so strikingly recalled the "kingsyellow worm" (Redia), found by Bojanus in pond-snails (Fig. 18), that one might almost believe "that this creature continued to live after the death of its jailor and perhaps grew into a similar form." Unfortunately this idea could not be proved, although its demonstration would have been of the greatest importance. Von Baer had previously shown that these Rediæ[4] gave rise, by a develop-

[1] *Oken's Isis*, p. 190, 1831.

[2] "Mikrographische Beiträge," Bd. ii., p. 140, Note, 1832.

[3] *Archiv f. Naturgesch.*, Jahrg. i., Bd. i., p. 69, 1835. Burdach, "Physiologie," Bd. ii., p. 208 : Leipzig, 1838.

[4] *Nova Act. Acad. Cæs. Leop.*, t. xiii., p. 627, 1826.

ment of germ-granules in their interior, to a brood of animals which resemble the tailed Trematodes, but, unlike them, swim about freely

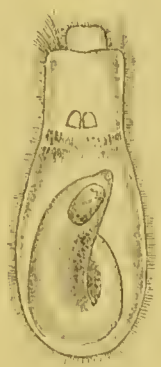


FIG. 17.—Infusorian-like embryos of *Monostomum mutabile* with the "necessary parasite."

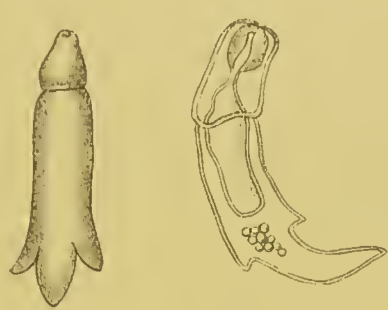


FIG. 18. — Bojanus' "kingsyellow worms" (Rediæ) from the pond-snail.

in water (Fig. 20), and had for this reason been included by the older naturalists among the Infusoria (under the name of *Cercaria*).

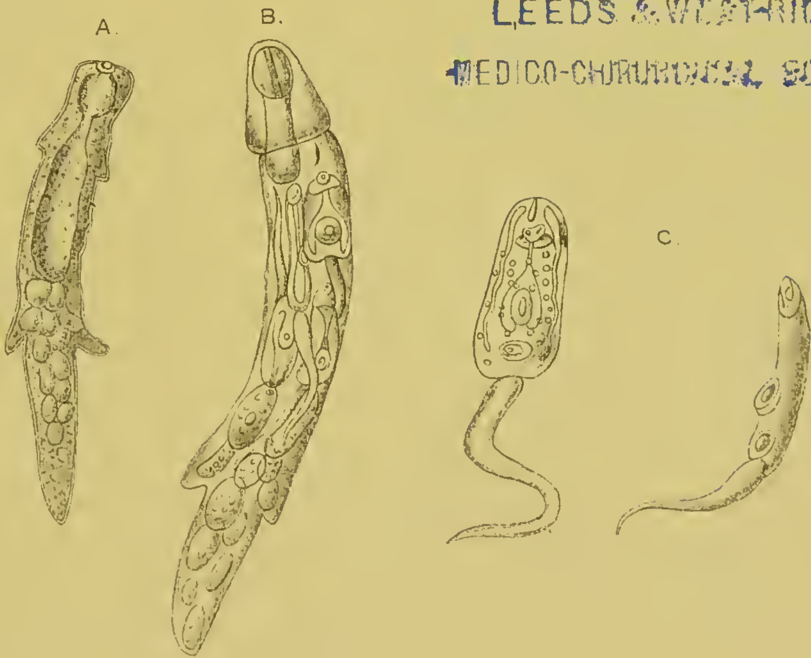


FIG. 19.—Rediæ. (A) with germs ; (B) with Cercariæ in the interior ; (C) free Cercariæ.

The investigations of von Siebold were not confined to the eggs of Trematodes, but were extended to the eggs of other intestinal worms, and led to the important discovery that in the tape-worms also the egg contained an embyro before it was laid. Here also the embryo was totally different from the parent, a simple spherical mass, distinguished only by the possession of six stylet-shaped hooks (Fig. 20) arranged in pairs at the anterior pole of the body, and capable of being moved like levers.[1] The subsequent changes undergone by this embryo were for some time uncertain, though there was no doubt that they could only pass into the fully formed animal "by a kind of metamorphosis."

Fig. 20.—Eggs of the tape-worm with six-hooked embryo.

Whether von Siebold perceived at that time the important bearings of his observations, must be left undecided. In any case, he neglected to follow them up to their legitimate consequences. This was done some years later by Eschricht,[2] who fully discussed the question of the origin of Entozoa for the first time since the days of Bremser, and who had also, in his masterly researches upon *Bothriocephalus latus*,[3] decidedly opposed the idea of spontaneous generation. In this work Eschricht collected all the facts that had been lately discovered about the metamorphosis of intestinal worms, and endeavoured to support the view that these phenomena were commonly found among the Helminths. He adduced the great development of the generative organs and the fertility of the Entozoa (the number of eggs produced annually by a single *Bothriocephalus latus* must be reckoned at at least a million, and of a female thread-worm at 64,000,000!) as evidence that did away with the enormous difficulties besetting the theory of a transmission to "suitable localities." Finally, he recalled the fact, first discovered by Abildgaard,[4] and also known to Bremser and Rudolphi,

[1] Burdach, "Physiologie," *loc. cit.* Previously to von Siebold, Göze had seen these embryos, but his description and figures ("Versuch, &c." tab. xxii., figs. 20-22,) are so insufficient, and for the most part so incorrect, that no conclusions can be drawn from them.

[2] *Edin. New Phil. Journal*, 1841.

[3] *Nova Acta Acad. Cæs. Leop.*, t. xix., suppl. 2, 1841.

[4] *Naturhistorisk Sclsk. Skrifter*, Bd. i., p. 53, 1790, ; see the remarks made on p. 24.

that *Bothriocephalus* (*Schistocephalus*) *solidus* and *Ligula* only attained to full development when they passed from the body-cavity of a fish to the intestine of a water-fowl, and stated that in all probability many other Helminths wander in a similar way from one organ of their host to another. By these and other facts, Eschricht arrived at the conclusion that *the life-history of Entozoa must be considered as analogous on the whole to that of the parasitic larvæ of ichneumon-flies and bot-flies,* but that each instance demands a special explanation, on account of the complexities possibly introduced. In the meantime, however, no details could be given, but in all probability the various asexual parasites so frequently met with encysted in the muscles and connective tissue, such as bladder-worms, *Filaria* (including *Trichina spiralis*), and *Echinorhynchus*—the latter being occasionally during the summer found in thousands in the flesh of fishes—must be regarded as immature forms, retaining their primitive larval situation.

We shall find later on that Eschricht had hit upon the truth in pointing out that change of place and of form were the most important facts in the life-history of parasites. But there were none of the necessary details forthcoming to prove his explanation, and it appears, therefore, in spite of his statements and the support which Valentin's[1] observations lent to them, that the majority of helminthologists continued to uphold the old theory of the spontaneous generation of intestinal worms.[2]

But gradually more and more light was thrown upon the obscurity which enveloped the whole subject of parasitic worms. Shortly after the publication of Eschricht's researches appeared Steenstrup's famous work upon the alternation of generations, which rendered intelligible so many facts in the developmental history of the lower animals that had been previously but incompletely appreciated. The discoveries and arguments brought forward by Steenstrup proved conclusively that there are animals whose descendants in the second or third generation return to the original form of the sexual animal, and that numerous intestinal worms belong to this class.

The proof of alternation of generations was most completely obtained from the Trematodes,[3] and quite simply, for Steenstrup connected their life-history with the above-mentioned Cercariæ. By discovering that these latter, in spite of their independent origin, were really larval Trematodes, he determined the fate of a large group of

[1] *Repertorium f. Anat. u. Physiol.*, Bd. vi., p. 50, 1841.

[2] Creplin, Art. "Enthelminthologie" in Ersch u. Gruber's "Allgem. Encyclop. d. Wiss.," Leipzig, 1818-1846, Bd. xxxv.

[3] "Ueber den Generationswechsel:" Copenhagen, p. 50, 1842. Translation by Ray Society, London, 1845.

parasites. Steenstrup was not content with solving the enigma merely by hypothesis; he also endeavoured by direct observation to place his opinions beyond any doubt. He discovered that these Cercariæ (Figs. 21 and 22) frequently made their way into the body of water-snails by boring through the muscular wall, and that, after losing their tails, they became encysted, resembling closely small and as yet asexual Trematodes. These facts were certainly not absolutely new, but those few naturalists who had anticipated Steenstrup in the discovery of the encysted condition of Cercariæ, erroneously formed the opinion that this process, instead of being the precursor of a further development, led merely to the death of the parasite. Moreover, Steenstrup himself fell into an error when he supposed that the tailless Cercaria arrived at complete maturity within the body of the original host; von Siebold,[1] who shortly after adopted the opinions of the illustrious Dane, rightly compared the development of the Cercaria to that of *Bothriocephalus* (*Schistocephalus*) *solidus* and *Ligula*, and believed that its further growth would not take place until the original host was devoured by some other animal.

FIG. 21.

FIG. 22.

FIGS. 21 and 22.—A free and an encapsuled Cercaria, the latter without tail.

The older investigators (von Baer, see p. 30) had already demonstrated the origin of the Cercariæ; but Steenstrup went further than his predecessors in showing the identity of the "kingsyellow worm" and the "living matrix of the Cercariæ" with the "necessary parasite" within the body of the embryonic *Monostomum*, though the resemblance had been previously pointed out by von Siebold. According to Steenstrup, the egg of the Trematode, expelled from the body of its host, gave rise to a free larva, which after a period of independent existence changed again into a parasite (the "generative sac") after casting its skin. This parasite, however, did not at once become a *Distomum*, but still remained a larval form (the asexual generation or so-called "nurse"), and in it was subsequently developed, asexually from germ-granules, another active larval form, the Cercaria from which the sexual adult then took its rise.

If it had been known before that the life-history of an animal could be divided into several cycles, this process of development would have been thoroughly understood some years earlier. The

[1] "Bericht über die Leistungen, &c.," *Archiv f. Naturgesch.*, Jahrg. xiv., Bd. ii., p. 321, 1848.

material was to hand, but there was no one capable of using it. In spite of the close similarity between the Cercaria and the *Distomum*, no one ventured to state that one was the young of the other, since they had been found in the bodies of quite different animals.

The phenomenon of alternation of generations threw a fresh light upon the well-known "sexless" Entozoa. According to earlier opinions, these were either independent, spontaneously generated organisms, or, as Eschricht thought, immature forms. The theory of alternation of generations rendered it possible that they played the part of an intermediate generation, the "nurse." In fact, Steenstrup[1] had no hesitation in speaking of many of these forms, especially the bladder-worms, as "nurses."

What stress was laid upon the migrations of the embryos by Steenstrup is sufficiently shown by his statement, based upon firm conviction, that the Entozoa are generally only parasitic for a longer or shorter period; and that at other times, perhaps in different stages or generations, they lead an independent existence, or, as it is termed, "have a geographical distribution in nature (*e.g.*, in water) outside the body of a host."[2] This opinion was strikingly confirmed by a new discovery.

Dujardin[3] frequently discovered on the ground, and especially after a sudden rainfall, masses of a *Filaria*-like Nematode (*Mermis*), resembling very closely *Gordius aquaticus*, which had been known for some time as an inhabitant of water. This appearance (the so-called "worm-rain") could only be explained by supposing that these creatures had left the bodies of insects or snails, upon which they are parasitic, for the purpose of laying their eggs in the damp earth. Von Siebold proved that this explanation was the right one, by finding not merely these Mermithidæ in the bodies of insects and insect larvæ, and observing them in the act of wandering away; but also by the discovery that *Gordius* was also sometimes parasitic.[4] At the time of their migration the Gordiaceæ are mature; but copulation and oviposition take place subsequently, in water in the case of *Gordius*, and in damp earth in the case of *Mermis*. Von Siebold succeeded later[5] in tracing the development of the embryo within the egg during the

[1] *Loc. cit.*, p. 111. [2] *Loc. cit.*, p. 116, Note.

[3] *Ann. Sci. Nat.*, t. xviii., p. 129, 1842. (Similar observations have been frequently made since the publication of this paper by numerous observers, and among others by myself.)

[4] *Entomolog. Zeitung*, p. 77, 1843. Villot has recently stated that the presence of *Gordius* in insects is an accidental wandering, while he believes that minnows and loaches are its normal hosts. See *Archives de Zool. Expér.*, t. iii., p. 182 *et seq.*, 1874.

[5] *Ibid.*, 1848, p. 290; 1850, p. 239,—*Jahresb. d. schlesischen Gesellsch. für vaterl. Cultur*, p. 56: Breslau, 1851.

winter, and proved that the young larvæ hatched in the spring make their way into the interior of young caterpillars, just out of the egg—an important addition to our knowledge of the life-history of Entozoa.

But before these observations had been brought to a close, von Siebold had already attempted to fashion the theory of the origin of the intestinal worms according to the newer views, which, as we have already seen, were receiving more and more support from the progress of discovery; and, with this end in view, he published a complete account of all the known facts relating to the development and generation of these animals.[1] This work, as might have been expected from the wide knowledge of the author and the well-deserved reputation he enjoyed as a naturalist, made a great impression, and spread abroad the conviction that the secrets of the phenomena of ento-parasitism were to be sought for in the migrations and transference of parasites, and were not explicable by any hypothesis of spontaneous generation. This work did not contain much that was absolutely new in the department of helminthology; for even the opinion

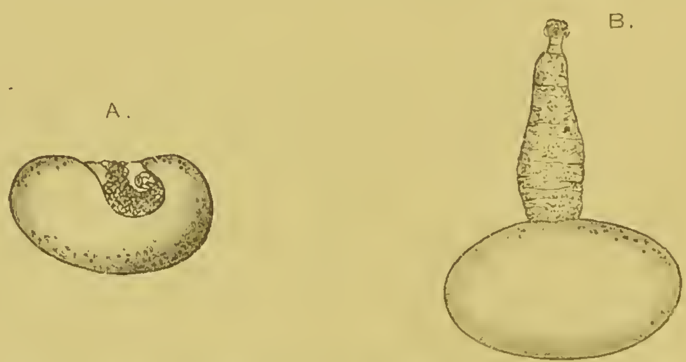


FIG. 23.—The common bladder-worm of the pig, with invaginated head (A), and with extruded head (B).

as to the tænioid nature of bladder-worms (Fig. 23) had been some time previously advanced by Dujardin, although it was treated of in detail for the first time in the article by von Siebold, and based upon the striking resemblance (already pointed out by Pallas and Göze) between the head of the bladder-worm of the mouse and that of *Tænia crassicollis* of the cat.[2]

Concerning the development of the bladder-worms, von Siebold had, however, peculiar views. He did not agree with Dujardin in regarding them as larval stages or "nurses," but considered them to be pathological formations caused by certain external circumstances,

[1] Art. "Parasiten" in Wagner's "Handwörterbuch der Physiologie," Bd. ii., p. 640: Brunswick, 1843.

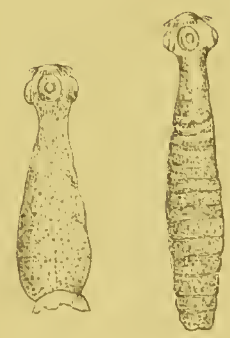
[2] "Hist. Nat. des Helminthes," pp. 544 and 632, 1845.

such as that the germ of the tape-worm had "lost its way"—that is, arrived at some place that was not suitable to its requirements. We shall have to examine this theory of "straying" later on, but for the present it may be remarked that von Siebold believed it to be of very wide application, and to explain the existence of many other sexless worms (even *Trichina*), which had not come to a full development on account of having strayed into unsuitable localities.

Later von Siebold made the developmental history of tape-worms the subject of a special memoir,[1] in which he sought to prove, with special reference to *Tetrarhynchus*, that the tape-worm heads found so abundantly encysted in predatory fish, originated from embryos that had wandered there, and that these developed into the sexual adult by the formation of segments (Figs. 24 and 25), when their host was swallowed by some other carnivorous fish in whose ali-

FIG. 25.

FIG. 24.



FIGS. 24 and 25.—*Echinobothrium minimum* (after van Beneden), isolated living head and tape-worm.

FIG. 26.—Transformation of the bladder-worm into a tape-worm (*Tænia serrata*).

mentary canal these chains of tape-worm segments were formed. Von Siebold based these arguments upon induction, but their correctness was subsequently certified by a direct proof of the metamorphosis and migration of these tape-worm heads.

Contemporaneously with von Siebold, or even earlier, van

[1] *Zeitschr. f. wiss. Zool.*, Bd. ii.; p. 198, 1850.

Beneden had investigated the Entozoa of various predatory fish, especially the shark and ray,[1] and made observations at all stages. He frequently found in the stomach of the shark the digested remains of various osseous fish with *Tetrarhynchus* heads, some of which were still encysted, some free or nearly so, while others had already buried themselves in the intestine of their new host, and budded out a longer or shorter chain of segments. Van Beneden's researches were so extensive, and dealt with so many different forms, that they fully justified the generalisation that the transference of asexual Entozoa takes place by means of the food of their host, which had been, up till the present time, only proved in the case of *Ligula* and *Schistocephalus*. It is not, however, our purpose here to enter particularly into van Beneden's statements as to the development of Cestodes; we shall recur to it in a future chapter, and content ourselves for the present with mentioning that a bladder-worm, according to this celebrated zoologist, is by no means a pathological condition, but is closely allied in structure and development to the head of a *Tetrarhynchus*.

The correctness of this opinion was soon verified by a new experiment, which showed that bladder-worms, as von Siebold had previously stated was the case in certain forms, after losing the bladder, become developed into true tape-worms in the intestine of a suitable animal (Fig. 26). The history of helminthology does not, perhaps, contain a single other fact that created such a marked sensation. It was, however, not merely the proof that bladder-worms, which had for so long a time formed an impregnable fortress for the theory of spontaneous generation, were really the immature stage of tape-worms, that excited so wide an interest, but it was also the circumstance that Küchenmeister,[2] the discoverer of this fact, did not discover it merely by chance, but by direct experiment, by the method of feeding, which is so easy to control and repeat, and has furnished the same results in other hands.

The idea of using this method of proving the nature of bladder-worms was suggested by previous discoveries, but it had, notwithstanding, been made use of by no observer. I say no observer, for the attempts of Klenke in this direction [3] have really not the slightest claim to be mentioned. The method has only proved of value in modern times. The meaning of helminthological experiment was

[1] "Les vers Cestoides": Bruxelles, 1850. (Preliminary account in the *Comptes Rendus Acad. Belg.*, 1849).

[2] "Ueber die Metamorphose der Finnen in Bandwürmer," *Prager Vierteljahrsschrift*, 1852.

[3] "Ueber die Contagiosität der Eingeweidewürmer:" Jena, 1844.

known to the older workers in this department. It has already been mentioned that Abildgaard in this way proved beyond doubt the migration of *Schistocephalus solidus* from the body-cavity of the fish to the intestine of the water-fowl. Also Pallas, Bloch, and Göze made the attempt to decide certain questions by the introduction of Helminths, or their germs, into various animals, without, however, getting any results of great importance.

Besides the widespread belief in spontaneous generation, which arrested so powerfully the progress of helminthology, the manifest unfruitfulness of the experimental method gradually caused it to drop into oblivion. It was reserved for Küchenmeister to reintroduce this method, and to show its importance for all time. A new and active vitality was thus breathed into helminthological science, so that observations and discoveries came thick and fast. Hardly a year had elapsed after the first trial of his method before Küchenmeister announced[1] that he had succeeded in obtaining bladder-worms from the bodies of animals fed with the ripe proglottides, and thus completed the whole cycle of the life-history of Cestodes.[2]

The earliest experiment was made upon a sheep which died before the complete maturity of the bladder-worms, obviously on account of the experiment. Without a thorough knowledge of the development of the bladder-worms, which was the condition of naturalists at that time, the result of the experiment might have been doubted, had not Haubner[3] and Leuckart[4] completely demonstrated that fact, by rearing almost all known bladder-worms, on an extensive scale, in suitable animals. But this experimental method was not confined to bladder-worms and tape-worms; it was also applied to other Entozoa, and in these cases also the same facts were strikingly shown.

De Filippi,[5] de la Valette,[6] and Pagenstecher[7] proved, by means

[1] *Günsburg's Zeitschr. f. klin. Med.*, p. 448, 1853.

[2] I am unable to understand how Küchenmeister can complain "that German science hardly thanked him for the services that he had rendered"—(This passage is reproduced from the first into the second edition of his "Parasiten des Menschen," 1878, Preface)—nor yet why he reproaches me with neglecting no opportunity of attacking him in an unfair manner. On the contrary, I feel satisfied that I have always plainly stated what science does owe to him in the way both of discovery and suggestion (see Preface to the first edition of this work, p. iv.). I have also corrected his unfortunately numerous errors, but only in those cases where it could not be avoided. Had I really wished to attack him, there was plenty of material at my disposal, at any rate more than Küchenmeister in his most recent work has endeavoured to bring up against me.

[3] *Gurlt's Magazin für ges. Thier-Heilkunde*, 1854 and 1855.

[4] "Die Blasenbandwürmer und ihre Entwickelung:" Giessen, 1856, p. 38 *et seq.*

[5] "Mém. pour servir à l'hist. génét. des Trematodes:" Turin, t. i.-iii.

[6] "Symbolæ ad Trematodum evolut. Hist.:" Berolini, 1855.

[7] "Trematodenlarven und Trematoden:" Heidelberg, 1857. "Ueber Erziehung von Distomum echinatum durch Fütterung," *Archiv f. Naturgesch.*, Bd. i., p. 246, 1857.

of experiment, that encysted Distomes grew mature directly after their migration from one host to another, as von Siebold had believed, and that in this way a migration to another host, or another organ, was necessary in the Trematodes, before they could attain to sexual maturity. Although hitherto the various stages of development of the same species had not been experimentally proved,[1] as in the Cestodes, we must regard our knowledge as having been completed by the experimental verification of this fact, and especially by Zeller's beautiful researches into the life-history of the ectoparasitic forms, especially *Polystomum integerrimum* of the frog,[2] which have completed our knowledge in another direction.

The parasitic Nematodes resisted investigation for a very long time. In the year 1863, when the first volume of my work on parasites appeared, I was only able to mention a single Nematode besides the Gordiaceæ just referred to (p. 35), whose developmental history was thoroughly known. This was *Trichina spiralis*, which Virchow's[3] and my own[4] researches showed to be developed in the intestines of rabbits, swine, and other Mammalia into a sexual form, which had previously escaped attention. The young of this worm are produced viviparously, and wander away from the intestine, becoming finally encysted in the well-known way in the muscles. Since this time, however, our knowledge has been considerably advanced by the observations recorded in the second volume of my manual. We are now acquainted not only with the life-history and migrations of the Acanthocephala, but also of numerous thread-worms belonging to different groups, and can show experimentally that the germs are extruded from the body of the host, and give rise to young, which, at a particular period of their existence, return to the body of their definitive host. Many of my further observations have greatly widened our conceptions of the parasitic mode of life, and have especially placed beyond a doubt the fact that *a change of host is by no means a necessity in the life-history of all Entozoa.* In many Nematodes, as we shall learn in the next chapter, the young stages are passed in an entirely free existence, and often (especially in certain Strongylidæ) under conditions similar to those enjoyed by free-living animals. The life-history of the Pentastomida shows, however, that a migration from one host to another is not confined

[1] Even the experiments of Wagner upon *Distomum cygnoides* leave a considerable gap in respect of its migration into the body of the frog, "Beitrag zur Entwickelungsgeschichte der Eingeweidewürmer," p. 29 *et seq.*: Haarlem, 1857.

[2] *Zeitschr. f. wiss. Zool.*, Bd. xxii., p. 1, 1872, and Bd. xxvii., p. 238, 1876.

[3] *Archiv f. pathol. Anat.*, vol. xviii., p. 330, 1860.

[4] *Zeitschr. f. rationelle Medicin*, Bd. viii., pp. 259 and 335, 1860.

to the Helminths. The development of these animals, which certainly closely resemble the Helminths in their parasitic mode of life, was worked out by myself some years ago;[1] I succeeded in rearing the so-called *Pentastomum denticulatum* in the intestine of the rabbit from the eggs of *Pentastomum tænioides*, and traced the development of the young *Pentastomum denticulatum* into the adult *Pentastomum tænioides* by placing the embryo in the nasal cavity of the dog.

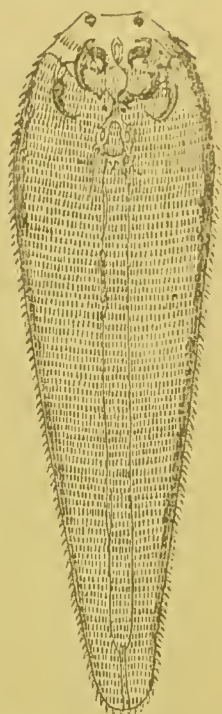


FIG. 27.—*Pentastomum denticulatum.*

Although these results of experimental helminthology appear so important and numerous, there yet remains much to discover. There are always forms, even among the most common of the Helminths, whose origin is unknown. We must admit that there is much in the natural history of parasites that seems problematical and hardly explicable, in accordance with our present experience, but who would dare, in the face of all the results that have been already achieved, to fill the gaps in our knowledge with the remnants of some antiquated theory? If Rudolphi and Bremser, and all the other champions of former helminthological theories, were present to-day, they would lower their colours, and refuse to renew the old disputes. The theory they fought for is an error that has been dissipated.

[1] "Bau und Entwickelungsgeschichte der Pentastomen:" Leipzig, 1860. Preliminary account in *Zeitschr. f. rationelle Medicin*, Bd. ii., p. 48, 1857; Bd. iv., p. 78, 1858.

CHAPTER IV.

LIFE-HISTORY OF PARASITES.

All that has been hitherto said about the origin, metamorphosis, and migration of parasites demonstrates plainly that the older observers, who denied any remarkable changes in their life-history, were entirely wrong. We now know that parasitism only represents a single phase in the life of an animal, which, in spite of its importance and extent in many cases, always presupposes another stage. In fact, if we only know concerning a certain animal that it is a parasite, we know but little; thoroughly to understand its history, we must follow out all the separate stages and conditions of its existence, and especially the circumstances under which it becomes a parasite.

However varied and numerous these may be, they are contained within fixed boundaries. There are certain standards, or rather certain types, of parasitic life, under which the individual cases are more or less definitely grouped. The knowledge of these conditions not only renders the individual cases intelligible, but it also enables us to cast a comprehensive glance over the whole field of parasitism, and therefore we may be thoroughly justified in prefacing the detailed study of individual types by a general sketch of their life-history.

We commence with the period of sexual maturity, since this leads to the beginning of a new life-cycle. Between different parasites there is a striking difference with respect to the sexual maturity; for, in agreement with what has already been stated concerning parasitism —that it is sometimes perpetual, and sometimes only temporary—we find some parasites whose period of sexual maturity coincides with the parasitic period, and others that do not attain to sexual maturity until they have commenced to lead a free existence.

On the whole, however, the last-mentioned class is but small, and contains only the larvæ of parasitic insects and the Gordiaceæ and Mermithidæ, so that it may be confidently asserted as a law, that parasites, and especially the Helminths, *attain sexual maturity while in the parasitic stage,* and therefore reproduce themselves in the body of their host. A closer examination shows that this fact is entirely in harmony with the conditions of parasitic life. The position of a parasite is—economically considered—most fortunate; its expenditure,

in locomotion and capture of its food, is small, generally less than in free-living animals, and the income, therefore, is large; there are in fact, without going into any further detail, numerous causes which must be considered as having a most important effect in furthering sexual maturity. The large balance on the side of income explains the great fertility, upon which stress has already been laid, as of extreme importance in the life-history of these animals.[1]

This, however, is merely *en passant*. Most important is the fact that sexual maturity and generation take place in most parasites during the time of their parasitic life. Copulation is often accomplished in the lower animals before the female is fully developed, and occasionally before the stage of parasitism commences. This is the case, at least, in the *Lernææ*, where coition takes place while the animals are swimming freely in the water,[2] and differ but little from the free-living Copepoda, and also in the chigoe (*Pulex* or *Rhynchoprion penetrans*, Fig. 28)—it being supposed, at least, that only stationary parasitism is to be taken into consideration. It is, moreover, as is well known, only the female that is a stationary parasite. While the male retains the ordinary form and habits of a flea, the female bores her way into the skin of the foot in man, dogs, and other mammals, and becomes, by the enormous development of the ovary, a simple, motionless bladder. It is improbable, however, that there is anything analogous to this in the Helminths. It was thought at one time (Carter), but wrongly, that the Guinea-worm was fertilised before it became parasitic; but, as a matter of fact, this Nematode is only found leading an independent existence in its earliest stages, when the sexual organs are totally undeveloped.[3] It is

[1] We may give this instance of remarkable fruitfulness, in addition to that of the Nematodes, to which allusion has already been made (p. 32). In *Tænia solium*, the contents of the uterus of each of the segments is about 6 cubic millimetres, and it holds some 53,000 eggs, each egg having a diameter of 0·06 mm.; seeing that a tape-worm produces yearly at least 800 segments, the total number of eggs will be thus some 42,000,000, a number that under favourable circumstances—(instances are known of tape-worms budding off five or six fresh segments daily)—is even occasionally exceeded. The extent of this fertility may be estimated by the following calculations:—The 64,000,000 eggs, which, according to Eschricht, a tape-worm brings forth in the course of a year, represent (each egg being ·05 mm. in diameter, and having a specific gravity equal to that of water), a mass of 41,856 mgrm. (1 egg = ·0000654 mgrm.). The adult worm itself weighs about 2·4 grm. or 3·4 grm., including the ovarian tube, and produces therefore yearly 174 gr. per cent. of eggs, about thirteen times as much as the queen bee, whose fertility is about 13 gr. per cent. A woman in giving birth to a child is deprived of about 7 per cent. of her weight, so that a thread-worm is as fertile as a woman would be if she brought forth seventy children every day!

[2] Claus, "Beobachtungen über Lernæocera, Peniculus, und Lernæa," *Schriften der Gesellsch. zur Beförderung d. ges. Naturw. zu Marburg*, Suppl.-Heft ii., p. 21, 1868.

[3] See Vol. II.

also questionable whether in this latter group parasitism is ever confined to the female alone, as has been very generally observed to be the case in the *Lernææ* and their allies. The simple fact that these are animals of which only the females [1] are parasitic is of great interest; this one-sided parasitism has never yet been observed in the male, except in the already quoted case (p. 10, note) of *Bonellia.* We must take into consideration here that only in a few cases is there a smaller expenditure in proportion to the production of sexual tissue, while for the female, on the contrary, the economic advantages of parasitism are of great importance. All that has been said concerning the coincidence of sexual maturity with the parasitic stage may be summed up in the following sentence:—*In the majority of parasitic animals the eggs are produced, fertilised, and deposited while they are in the parasitic stage.* Although it is usually the case that the eggs are deposited in the host in which the parasite dwells, there are a few exceptions, such as many *Tæniæ,* where the eggs remain in the proglottides and are extruded from the body of their host.

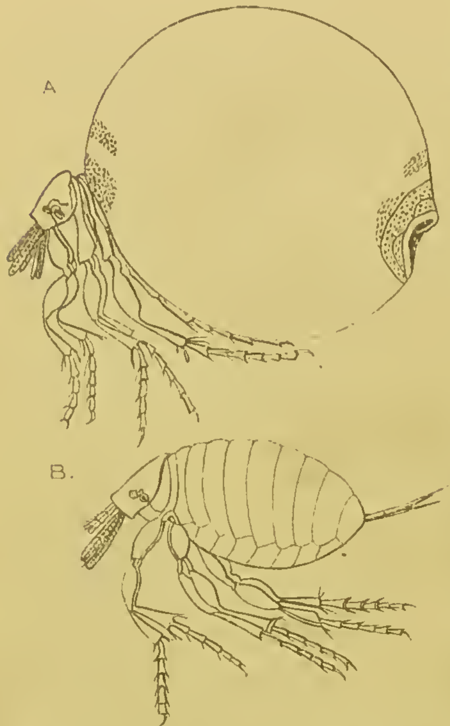


FIG. 28.—*Pulex penetrans.* *a.* Female. *b.* Male.

EGGS AND EMBRYOS.

In general the eggs of parasites are deposited in those places where the parent lives; thus the Epizoa lay their eggs upon the outer skin; the intestinal parasites deposit them in the intestine of their host, and so on. In some cases, however, at the time of oviposition, parasites undertake special migrations like free-living animals. There is a human parasitic worm that does so—*Distomum hæmatobium* (Fig. 29); this worm usually lives in the portal vein, but when sexually mature, as we learn from Bilharz, migrates in pairs, the female being

[1] In the same manner the sucking of blood by the Culicidæ is confined to the females. The males possess a suctorial apparatus with which they can take up fluid nourishment, but it is not so strongly developed as to enable them to pierce the skin. See Dimmock on "The Anatomy of the Mouth-Parts of some Diptera," p. 20: Boston, 1881.—R. L.

contained in a groove on the lower surface of the male, into the veins of the pelvis, where the eggs are deposited in masses.

With respect to the stage of development which the eggs have attained when they are laid, the differences in various species are considerable; every stage, from the egg just fertilised to that which contains a fully developed embryo, is represented. According to the length of time which the fertilised egg passes in the ovarian duct, it is either unchanged, or has commenced to segment, or may even contain a fully developed embryo; it happens sometimes, *e.g.*, in *Trichina spiralis*, that the embryos are hatched while in the body of their mother, which thus becomes viviparous instead of oviparous. It is not uncommon to find all these different ways in animals very closely allied, and it follows therefore that the mode of giving birth to its young affords no clue to the systematic position of a parasite. Quite as varied also is the subsequent history of their eggs; in some cases they remain for a long period—almost until the young are hatched—in the identical spot where they were deposited; while in other cases they are immediately extruded from the body of their host, and undergo their further development at large. The latter is the most usual, and may be taken for granted where circumstances favour the dispersion of the eggs. There are numerous exceptions in individual instances, especially among the Epizoa, which often deposit their eggs in a more or less elaborate manner upon various processes of the body (lice, for instance, attach their eggs to hairs; *Dactylogyrus, Diplozoon*, &c., attach them to the branchiæ of their host). When in such cases the ordinary means of attachment are not sufficient, the egg-shell is provided, as in the species just mentioned, with some special apparatus of attachment in the shape of suckers or tendril-like processes. These structures are as important to the eggs of parasites as the various similar structures already alluded to (p. 6) are for the parasite itself.

Fig. 29.—*Distomum hæmatobium*, male and female, the latter in the canalis gynæcophorus of the former.

It very commonly happens among intestinal parasites that the eggs are early extruded from the body of the host, since they are continually being pressed onwards by the semi-fluid contents of the intestine; this is so often the case, that we are not acquainted with a

single parasite [1] that undergoes all its life stages without a change of locality. The number of eggs evacuated with the fæces varies of course with the fertility and the number of the parasites, and is sometimes so considerable, that a very superficial microscopic examination is sufficient to show their presence. Moreover, the intestinal parasites are not the only ones whose eggs are evacuated; the same thing takes place in animals living in other organs—the eggs of *Distomum hepaticum* reach the intestine through the bile duct, and are thus shed from the body. In the same way the eggs of the bronchial parasite of the sheep, *Strongylus filaria*, are removed with the tracheal mucus, and the eggs of *Pentastomum tænioides*, which lives in the nasal cavity of the dog, leave the body along with the secretion of the Schneiderian membrane; the eggs of *Strongylus gigas* and the embryos of *Filaria Bancrofti* are passed out along with the urine.[2] Nor is it necessary that the parasites should live in organs that are in direct communication with the exterior; there are instances where such communications are made by some subsequent abnormal process. The eggs and embryos of *Distomum hæmatobium* break through the wall of the urinary and rectal blood-vessels in which they are originally laid, into the surrounding spaces, where they form abscesses. The same thing is seen in *Stephanurus* (the "kidney-worm" of the Americans), which lives near the kidneys in swine, and bores its way into the pelvis of the kidney. The embryos of *Dracunculus* (*Filaria Medinensis*), which, as is well known, live between the muscles, reach the exterior through an abscess, which is formed as soon as the head of the worm comes into contact with any part of the cutis.

If we bear these and other similar cases in mind, and also keep in view the fact that by far the greater number of sexual Helminths live in the alimentary canal, it is evident that we are right in considering the widespread occurrence of these migrations to be important in the life-history of parasites. But those other cases, where the eggs remain upon the spot where they were deposited until the escape of the young, become, on this account, all the more striking and interesting. We have already mentioned that, to attain this latter end, the eggs of the Epizoa are fastened in various ways to the outer skin. There is no need of anything of this kind in the internal organs, where the inaccessibility of the position

[1] In the German text *Anguillula* (*Rhabditis*) *stercoralis* was here mentioned as an exception, but, as above mentioned (p. 21, footnote), this form has proved to be merely a developmental stage of a parasite already known under the name of *Anguillula intestinalis*.—R. L.

[2] A proper microscopical examination of the fæces and excreta under such circumstances generally furnishes a reliable diagnosis.

is sufficient of itself to ensure the safety of the eggs. In these cases the eggs are usually laid in the tissue in masses, which are often so large that they form conspicuous tubercle-like bodies—the so-called "worm-nests" or "worm-knots." Formations of this kind are often met with in the lungs of mammals, especially of sheep, oxen, and rabbits, sometimes in such profusion that inflammation sets in, and soon kills the animal.[1] Actual worm epidemics are sometimes caused in this way. The parasites which lay the eggs belong to the Strongylidæ[2]—(in the sheep, *S. filaria*; in the ox, *S. micrurus* and *S. rufescens*; in the rabbit, *S. commutatus = Filaria leporis pulmonalis* Fröhl.)—a group of thread-worms which are commonly found in the trachea and air passages of our domestic animals, and also occasionally of man.[3] Some species of *Filaria*, in like manner, form "worm-knots." Ecker[4] records the discovery in a rook of a tumour as large as a pea, which contained a full-grown *Filaria attenuata* and a mass of its eggs. Generally, this species is found free in the intestine of its host, or in the loose connective tissue, under conditions unfavourable to the accumulation of large masses of eggs. This phenomenon, exceptionally found in *Filaria attenuata*, is very general in other members of the same genus. Thus, *Filaria sanguinolenta* of the dog, which in hot countries is found in almost every third individual, occurs on the aorta and the œsophagus in the sexual condition, massed together in great quantities, with eggs in every stage of development.[5]

Nothing of the kind has been hitherto observed in man, with the exception of the egg-masses of *Distomum (Bilharzia) hæmatobium*, in the veins of the urinary organs, which only continue for a short time. There are some descriptions of worm-knots in the human body, but the evidence is not quite satisfactory.[6]

[1] Bugnion ("Sur la pneumonie vermineuse des anim. domest.," *Comp. Rend. Soc. Helvét. à Andermatt*, 1875), places with these cases the cysts of *Ollulanus*, described by me (see Vol. II.) in the lung of the cat. He believes, in opposition to my views, that these are not formed by embryos which have lost their way and died, but considers them—as did also Henle, who was the first to describe a case of this kind (*Allgem. Path.*, Bd. ii., pp. 789 and 798)—as eggs in various stages of development. Since Stirling ("On the Changes produced in the Lung by the Embryos of Ollulanus tricuspis," *Quart. Journ. Micr. Sci.*, N.S., vol. xvii., p. 145, 1877) has confirmed my opinion, I need say no more about Bugnion's views. I may also mention the fact that occasionally *Ollulanus* causes worm epidemics.

[2] Vol. II.

[3] Diesing described a certain *Strongylus longevaginatus*, from the lungs of a child that had died of pneumonia (see Vol. II.) which is probably identical with *Strongylus paradoxus* from the lungs of the pig.

[4] *Archiv f. Anat. u. Physiol.*, p. 501, 1845.

[5] Lewis, "The Pathological Signification of Nematode Hæmatozoa:" Calcutta, 1874.

[6] In the case quoted by Gubler (*Gaz. méd. de Paris*, p. 657, 1858, and, in detail, *Mém. Soc. Biol.*, t. v., p. 61, 1859), the bodies thought to be the eggs of Helminths were

It is, moreover, not without significance that all these cases of "worm-nests" belong to the Nematodes. Seeing that it is an undoubted fact that there are parasites whose eggs remain, without further development, in the same place where they were deposited, and are not extruded from the body, as is the rule in other cases, the fate of the embryos that arise from such eggs remains to be examined. The most evident supposition is that these embryos grow to maturity in the same spot by the side of their parent, and this is quite true of certain parasites. It is well known, for instance, that the young lice grow to maturity on the spot where they were born, and the investigations of Wagner, Zeller, and myself have shown that this is also the case with the above-mentioned gill-parasites, at least *Dactylogyrus*, *Diplozoon*, &c.

Fig. 30.—*Rhabditis terricola?*

The life-history of such parasites thus becomes extraordinarily simple. One generation follows another without any change being necessary, either to another host or another organ. If there be any migration, it is due to a mere accident.

So far as we know, it is only Epizoa which have a simple life-history of this kind, though it has been attempted to prove that certain entoparasites, especially thread-worms, reach maturity without a change of locality. This opinion has, however, been shown to be incorrect, even in the case of the maw-worm (*Oxyuris vermicularis*), which is generally found in vast quantities in the human alimentary canal, and on that account would seem most apt to support such a theory.[1]

Neither has the statement of Norman been confirmed, according to which all the developmental stages of *Anguillula* (*Rhabditis*) *stercoralis* should be abundantly met with in the viscera of persons suffering from "Cochin-China diarrhœa." This worm is, as above

in reality Psorosperms (*Coccidium*, Lt.), which used frequently to be mistaken for eggs (see *postea*). Virchow described (*Archiv f. path. Anat.*, Bd. xviii., p. 523) a genuine case from the liver; the eggs, however, proved not to be *Pentastomum*, as Virchow thought, but *Ascaris lumbricoides*, from an examination that I made of some specimens that were sent to me, which were previously forgotten. Thus there is one case of the presence of a thread-worm in the bile duct (see Vol. II.) So, too, with the "worm-nests" of *Trichosomum* described by von Siebold in the spleen of a shrew-mouse (*Archiv f. Naturgesch.*, Jahrg. xiv., Bd. ii., p. 358, 1858). The bodies of the worm were found twisted together in knots near the eggs.

[1] In support of this statement, which is at variance with the opinions of Küchenmeister ("Parasiten des Menschen," first ed., p. 229) and Vix ("Ueber Entozoen bei Geisteskranken," *Zeitschr. f. Psychiatrie*, Bd. xvii.), I may quote my own observations described in Vol. II. of this work, which have also been confirmed by Zenker (*Abhandl. der physik. med. Societät zu Erlangen*, Hft. 2, p. 20, 1872).

mentioned, no true parasite, but the mature state of a heteromorphous species, the so-called *Anguillula intestinalis.* The young are born in the intestine of the host, and attain maturity (like *Rhabditis*) only after abandoning the latter; they live in the same way as *Rhabditis terricola* (Fig. 30), and then give rise to a new generation.[1]

It appears, therefore, that the following generalisation may be safely made:—*There are no intestinal worms,* at least among the typical and constant parasites, *whose embryos come to maturity near the parent;* or, in other words, *there are none which pass their whole life-cycle in one locality.*[2]

If we now turn to the embryos arising from these so-called worm-nests, it seems clear that they by no means reach further development in the body of their host, but after a longer or shorter period abandon it for a free external life. All the little that we know by direct experiment agrees with this. Ecker discovered in the body-cavity and blood-vessels of his rook numerous small *Filaria*-like Nematodes, which he considered to be the embryos of *Filaria attenuata,*[3] and he found them in a later stage as small worms measuring about a line, encysted in the mesentery and other places. Vogt has made similar observations;[4] he discovered in the body-cavity of a frog two large *Filariæ,* more than an inch long, containing numerous embryos; the latter he also observed circulating in the blood. Lewis has also shown that numerous Hæmatozoa are found in dogs afflicted by *Filaria sanguinolenta,* and the same thing was observed by Gruby and Delafond;[5] and later by Leidy and Walch,[6] in cases where *Filaria immitis* was present in the right heart of the same animal. In the case last mentioned the embryos have no difficulty in getting into the blood, since they inhabit from the first an organ which they could reach otherwise only by means of an active migration.

[1] Leuckart, "Lebensgeschichte der sog. Anguillula stercoralis, u. deren Beziehung zu d. sog. A. intestinalis," *Bericht math. phys. Cl. k. Sächs. Gesellsch. d. Wiss.*, p. 85, 1882.

[2] I use the term "intestinal worms" instead of "Entozoa" advisedly, since among Gregarine parasites there are many which regularly reach maturity near their parents. In other cases, where the germs grow to embryos at large, there is a regular migration, as in intestinal worms, to and from the body of their host.

[3] Hæmatozoa, arising from *Filaria attenuata*, are very commonly met with at Leipzig. Of 38 crows which Kahane examined for this parasite at my suggestion, 28—*i.e.* 80 per cent.—contained it, and sometimes in such abundance that the smallest drop of blood contained quantities of them. By examining a certain amount of blood, the weight of which had been previously ascertained, it was found that 1 mgrm. of blood contained 601 embryos, which means that the whole of the blood, reckoning it at $\frac{1}{12}$th of the whole 360 gr. net weight, would contain about 18,000,000.

[4] *Archiv f. Anat. und Physiol.*, p. 189, 1842.

[5] *Comptes Rendus*, t. xlvi., p. 1217, 1858.

[6] *Monthly Micr. Journ.*, p. 157, 1873.

The Nematode Hæmatozoa have lately attracted considerable attention by their discovery in man (Fig. 31), under circumstances

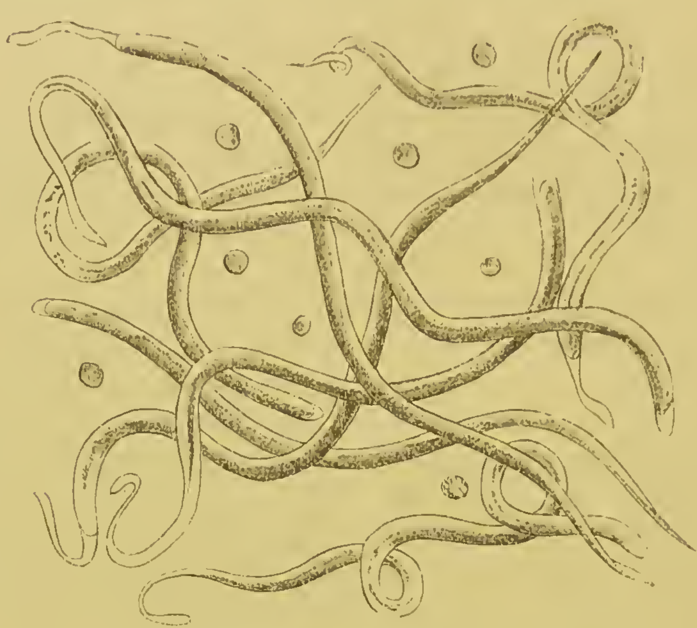


FIG. 31.—*Filaria sanguinis hominis* (after Lewis).

where they must have a considerable pathological signification. The Nematode appears to be very widely distributed in the tropics of the new[1] as well as the old world. The first discoverer of this human Hæmatozoon was Lewis of Calcutta,[2] and he regarded it at first as an adult parasite (*Filaria sanguinis*); but subsequently considered it to be the young form of a *Filaria*-like worm,[3] which, in the sexual state (as *F. Bancrofti*, Cobb.), is found viviparous in the subcutaneous connective tissue, more especially of the scrotum.

[The embryos of this worm probably reach the blood through the lymphatic system. According to Manson's interesting discovery they were usually found in blood only at night, and appeared to be entirely wanting during the day. At midnight the number of these embryos in the blood attained its maximum.[4] Such at least is the case when the patient preserves the usual order of life, but the reverse happens if he sleep by day and wake by night.[5] This proves satisfactorily that the periodical appearance of

[1] Since Magalhaes (*O progresso medico*, Rio de Janeiro, p. 375, 1878,) has discovered in blood the urinary worm of Wucherer, I cannot doubt that the Brazilian form is identical with the Indian parasite. The worm has also been observed in Japan and Australia.

[2] "On a Hæmatozoon inhabiting Human Blood," Calcutta, 1872. Ed. 2, 1874.

[3] *Centralblatt f. d. medicin. Wiss.*, No. 43, 1877; more in detail—*Lancet*, Sept. 1877, p. 453. See also Cobbold, *ibid.*, p. 495, and Vol. II. of this work.

[4] Manson, *Journ. Queckett Micr. Club*, vol. iv., p. 239, 1881.

[5] Mackenzie, *Lancet*, August 27, 1881.

the worms is to be explained by the state of the host as regards digestion and muscular exertion, as well as on the motion of the lymph due to these.[1]—R. L.]

If these Hæmatozoa arrived at complete maturity in their host, one would expect to find, not merely a vast and increasing number of adults, but also all the intermediate stages. But no one has hitherto observed anything of the kind; the Hæmatozoa remain for months, and even years (Gruby and Delafond), in the same developmental stage, and without altering in size. Even in cases where the adult worms exhibit some variation in their stages of development, as Lewis observed in certain parasites of the dog, there is a considerable gap between the youngest of these and the Hæmatozoa in the blood. These facts point to the conclusion that the intermediate stage between the Hæmatozoon and the fully developed parasite is passed outside the body of the host.

The analogy of *Trichina* also lends support to this opinion. The young of this Nematode are produced viviparously, and like the embryos of the above-mentioned *Filaria*, wander about in the body of their host,[2] the only difference—and that an important one—being that they abandon the blood-vessels and betake themselves to the intermuscular connective tissue. In both instances we have a wandering from one part of the body to another, though it differs in kind in the two forms. But in *Trichina* also the result of this wandering is by no means the direct degeneration into the parasitic condition of the adult; the embryos, on the contrary, remain within the muscles, and, after developing up to a certain point, become encysted, and remain in this condition (as muscle-*Trichinæ*, Fig. 15) until they are swallowed by a new host, when they recommence their wanderings.

In *Trichina*, therefore, and in these Hæmatozoa, a change from one host to another is necessary before sexual maturity can be reached. From the observations of Ecker, that the Hæmatozoa of the rook encyst themselves in the mesentery of their host, one would be inclined to believe that the life-history of *Filaria attenuata* is to be regarded exactly in the same light as that of *Trichina*, and that the transference into a new host is brought about by the encysted form. I myself, however, believe that this is really not the case, and that the encysted worms have nothing to do with the developmental cycle of *Filaria attenuata*, not merely because in this event they ought to be far more abundant than they actually are, but because the contents of these cysts, in the instances that I personally examined, agreed entirely

[1] Scheube, "Die Filarien-Krankheit," in Volkmann's "Sammlung Klinischer Vorträge," No. 232, Leipzig, 1883.

[2] Leuckart, "Untersuchungen über Trichina spiralis," Leipzig, 1860. 2d ed., 1865.

with certain Nematode larvæ, which are present in the same situation in other birds, entirely free from *Filaria attenuata* or any other Hæmatozoa.

The Hæmatozoa, then, after a longer or shorter sojourn in the blood-vessels, would appear to leave the body of their host in some way or other, and continue their life-history under other conditions. This supposition is strongly supported by what has been observed in human Hæmatozoa. According to Lewis, these worms bore through the capillaries of the kidney and make their way into the renal tubules, and thence to the exterior. [This emigration takes place so rapidly that, after a day has elapsed, in most cases very few worms, sometimes not even one, can be found, unless a fresh introduction have taken place. The significance of this migration to the future development of the worm is still unknown.—R. L.] Up to the present, this observation is certainly unique, and nothing similar has been observed in the Hæmatozoa of other animals, though investigations have been carried on.[1] If future researches throw no fresh light upon the subject,—and it is always possible that the emigration is different and more difficult to observe than in man, whose urine contains in abundance not only the Hæmatozoa, but also a quantity of blood and albumen mingled with them, which renders their presence obvious—there always remains the possibility that the Hæmatozoa continued to live in the blood, without change, until set free by the death of their host, which enables them to undergo further metamorphosis; and this is rendered more possible by the fact that no one has succeeded in finding the worms that originate from these Hæmatozoa in any animals where the latter are present,[2] and it is evident that they must at some time or other have been there.

We have hitherto been considering those embryos only which, after being hatched, remain for some time in the body of their host; but these are only a small number of examples. The general rule is, that *the eggs, as soon as they are laid, are evacuated from the body of their host together with its excreta*, and undergo their further development in various places and under various conditions, as chance directs.

[1] Borrell (*Archiv f. pathol. Anat.*, Bd. lxv., p. 399, 1876) shows reason to believe that the Hæmatozoa of the crow leave the body by the bile-duct, but the above-quoted investigations of Kahane prove that no *Filariæ* are present here, or in the cloaca, ureters, or bronchi, except, of course, there has been some mixture of blood.

[2] Gruby and Delafond only found once, in twenty-four dogs infested with Hæmatozoa, the *Filariæ* from which these originated. According to Ercolani, *Filaria mitis* is to be found not only in the heart, but also in the connective tissue under the skin, where it might be easily overlooked (Rivolta, "Studi fatti nel gabinetto di Pisa," 1879). Similarly, among the above-mentioned thirty-eight crows, there were only three in which the presence of *Filariæ* could be proved; of course it is probable that the sexually mature worms may have escaped observation, here and there, on account of their concealed position.

In many cases, however, the circumstances and environment are by no means favourable. It may be stated generally that some degree of moisture is necessary to ensure further growth. In dry localities, the eggs lose their power of development, not merely for the time, but permanently, while in damp localities and in water they retain this power for a considerable period. In this respect the eggs agree with the full-grown animals, as do also, even to a greater degree, the embryos, which are frequently hatched in the body of the host and then evacuated.

We cannot, however, make a hard and fast rule, since there are a number of Helminths whose eggs and embryos can withstand complete desiccation with impunity: these are chiefly Nematodes, a group which will be considered later on. The Nematoda, in spite of the simplicity of their organization and development, or perhaps rather because of it, display a variation in the conditions under which they live greater than that of any other group of Helminths. Not only are there parasitic, semi-parasitic, and free-living species, but numerous others, that infest plants, in many of which (wheat, rye, teazle, and clover) they give rise to actual diseases. That these parasites are liable to undergo a process of desiccation at regular intervals is hardly surprising, considering the periodicity of the developmental cycles of the plants which serve as their hosts. As an instance may be cited the wheat-grains which are infested by the young of a Nematode. When the seed is sown, the young parasites are brought into conditions favourable for their migration and further development.[1] This capability of withstanding desiccation is not, however, confined to Nematodes parasitic upon plants, but is occasionally found in those species that infest animals.

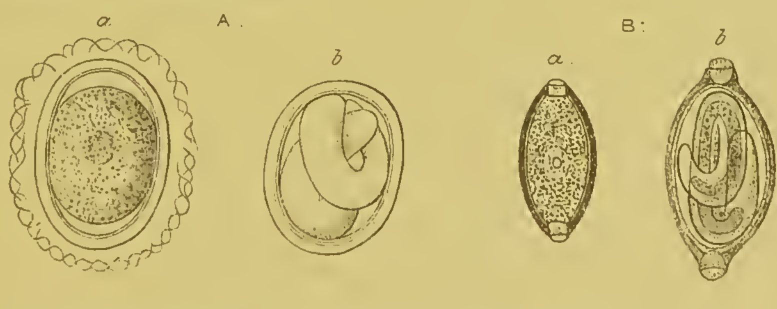


FIG. 32.—*A*, Eggs from *Ascaris lumbricoides*, and *B*, *Trichocephalus dispar*; *a*, fresh from the fæces; *b*, after long exposure to the open air.

To investigate the influence of desiccation upon the capability for development possessed by the eggs of Nematodes, I have made use

[1] See the excellent researches of Davaine on *Anguillula tritici.*, *l'Instit.*, p. 330, 1855; or (more in detail) *Mém. Soc. Biolog.*, t. iii., p. 201, 1856.

of a simple piece of apparatus consisting of a ring of blotting-paper enclosed between two glass slides. By alternately damping and drying the paper, the eggs could be brought into a moister or drier atmosphere. The conclusion to which I have been led by the use of this apparatus is, that the eggs of numerous Nematodes (Fig. 32), especially those with a thick shell (*Ascaris lumbricoides*, *A. megalocephala*, *A. mystax*, and many free-living Rhabditidæ), are not merely capable of enduring a complete desiccation lasting for weeks and even months, but also alternations between the moist and dry conditions. Development does not proceed, however, save in a damp environment, but it is sufficient that the air be merely moist; indeed, it has appeared to me that this is actually more favourable than wetting the eggs themselves with water. In damp earth development advances rapidly, but if the earth be dried, development is at once checked, without, however, destroying the vitality of the germs.[1]

The same holds good for the embryos; by desiccation they are rendered quiescent, but resume their vital functions on being moistened, as has been known for some time with respect to those species with free-living young (*e.g.*, *Filaria Medinensis* and *Rhabditis*). But all the experiments are not opposed to the general law that *a moist environment is necessary for the further development of the eggs of Entozoa.* Of course this is not the only necessary condition. The degree of this moisture, the nature of the environment in other respects, its chemical composition and temperature, are factors which are of varied importance in different cases. Unfortunately, our knowledge on these points is defective, but one fact may be stated with confidence, and that is, that the eggs of certain Nematodes, especially those having a thick shell like *Ascaris*, possess an extraordinary power of resistance, and can remain a long time without injury to the development of the embryo[2] even in spirit, turpentine, chromic acid, and various poisonous liquids, fatal to the fully grown worm (Bischoff, Leuckart, Munk). Sometimes the degree of concentration of the liquid has an effect. Vix found that the eggs of *Ascaris* were destroyed by a solution of soap of 0·5 per cent., while in a solution of 1 per cent. they continued to develop. Similarly, as I have experimentally demonstrated, by means of small holes, artificially dug in the earth and filled with decomposing fæces and urine, the eggs of *Ascaris lumbricoides* are gradually destroyed; they are likewise often destroyed through the foulness of the water which surrounds them.

[1] The statement of Davaine (*Mém. Soc. Biolog.*, t. iv., p. 272, 1862), that the eggs of *Ascarides* inhabiting terrestrial animals undergo development when dried up, rests upon an error.

[2] This is the case also with the so-called Psorosperms, which are the germs of Gregarinoid parasites (*Coccidium*, Lt.).

All that these experiments show is that there is a limit to the power of resistance possessed by the eggs of Nematodes.

All the cases just cited, however, by no means lead us to infer that power of resistance is not shown by the eggs of other Helminths, though certainly they do not show it to so great an extent as the Nematoda; but, compared with other animals, unfavourable conditions of environment take a much longer time to destroy the eggs, and this is no doubt owing rather to the simple fact that the shells of the eggs of these parasites are unusually thick, than to any peculiarity in their protoplasm. In this connection it is important to notice that the eggs of Helminths are not only usually provided with a thick firm shell, but frequently possess in addition a simple or more complex accessory covering of some kind, which occasionally gives them a remarkable and characteristic appearance. This additional protective covering, besides serving to increase their power of resistance, often has other functions; for example, the eggs of *Pentastomum tænioides*, which inhabits the nasal cavity of dogs, have a folded outer layer which enables them to adhere to various bodies when they are ejected from the nose of their host. In a similar way the various filamentous or tufted prolongations of the outer egg-shell (Fig. 33), or the coating of albumen which is sometimes to be found (Fig. 32 *a*) on the egg-shell proper, serve to secure the attachment of the egg to any body with which it comes in contact. The eggs of *Tænia* frequently leave the body of their host enclosed in a living covering—the proglottis—which possesses a certain capability of locomotion, and therefore aids considerably in the dispersion of the contained ova, which are thus rendered more independent of external agents. In spite of all these arrangements, thousands of the eggs of Helminths are destroyed by the unsuitableness of the environment; but this is of no importance, considering their immense fertility.

Fig. 33.—Egg of a tape-worm from a bird, *Tænia nymphæa*.

Assuming that the eggs attain to favourable conditions, let us now trace out the further course of their development. In the first place it must be remembered that the eggs reach the exterior in very different stages of development; in many instances (*e.g.*, Acanthocephala, *Tæniæ*, many Distomidæ, &c.) the embryo is already formed; in others, again, the egg contains merely the original cell. The presence of an embryo, however, is the preliminary condition of any further change. The eggs that, when extruded from the body of their host, are either not at all or only incompletely developed, at once undergo the process of forming the embryo, and the young is hatched.

This is known to be the case especially in the eggs of Nematodes, which were not only hatched, according to Schubart and Richter, in small aquaria, but also, as already mentioned, in a damp atmosphere and damp earth with even greater certainty. This has also been proved in the case of the eggs of numerous tape-worms (*Bothriocephalus*) and Trematodes.

In many, almost in the majority of instances, embryonic development only progresses during the summer months, and in many species only under the influence of a considerable degree of warmth; thus the eggs of *Ascaris lumbricoides* require a temperature of 20° C., those of *Trichocephalus* 22·5° C., and those of *Oxyuris vermicularis* as much as 40° C. The eggs of the latter develop a complete embryo in a few hours, and when the temperature is increased, in a still shorter time,[1] while the eggs of *Ascaris* and *Trichocephalus*, which differ from those of *Oxyuris* in being entirely undeveloped at the time that they are laid, require several weeks; and when the temperature varies, as it generally does in this country in the summer, several months elapse before the young are hatched. *Trichocephalus* rarely completes its development within the year; *Ascaris lumbricoides*, in the natural course of events, requires three or four months, and *Ascaris mystax* some three weeks. On the other hand, the young of *Dochmius duodenalis* (especially in warmer climates) are hatched in a few days. Similar variations are found in Trematodes and Cestodes, the eggs being sometimes hatched in a few days (*Triænophorus*), at other times requiring weeks (*Ligula*) or even months (*Bothriocephalus latus*, *Distomum hepaticum*, &c.) for their full development. This, however, only applies to the summer months; in winter, even in a heated chamber, development goes on slowly and irregularly; in *Ascaris mystax*, for example, the first traces of cleavage appear only after several months.

FIG. 34.—Eggs of *Oxyuris vermicularis*; *a*, *b*, freshly laid; *c*, with developed embryo.

Besides temperature, other circumstances are of considerable importance. There are individual differences between eggs themselves; embryos rarely develop in them simultaneously; one egg may have hardly commenced to divide, while another contains a fully formed embryo. Numerous eggs also, under conditions favourable in other respects, never develop, but undergo a process of degeneration in which the whole mass becomes granular and semi-transparent, and all the details of its structure vanish. It may be that these eggs

[1] In sunshine Vix saw an active embryo develop in a quarter of an hour in the eggs of *Oxyuris*.—*Zeitschr. f. Psychiatrie*, Bd. xvii., p. 65, 1860.

have never been fertilised, and this view is supported by the fact that the eggs of unfertilised females among the Nematoda degenerate in the same way without any apparent cause.

In Entozoa that develop in a short space of time (*e.g.*, *Doehmius duodenalis*), the early stages are usually passed through while the eggs are traversing the alimentary canal of their host. Occasionally the whole process takes place in the body of the host, especially when they remain there for a considerable period. A longer sojourn in a living host may thus be a necessary preliminary to embryonic development.

Though our knowledge with regard to the germinal activity of the eggs of Entozoa rests at present upon a comparatively small number of experiments and observations,[1] these are so entirely in harmony, that there is no doubt about the general facts. We can therefore state with confidence that the embryos of oviparous forms develop after the eggs are laid, while those of viviparous (or ovo-viviparous) forms are developed previously,—in other words *the eggs of all parasites at some time or other, either sooner or later, develop an embryo,*[2] *provided that they meet with favourable conditions.*

MIGRATION OF THE YOUNG BROOD.

The embryos of Entozoa by no means exactly resemble their parents. On the contrary, they never do so, even in the Nematodes,

FIG. 35.—Egg of *Distomum hepaticum* with embryo.

FIG. 36.—Egg of *Bothriocephalus latus* with embryo.

FIG. 37.—Egg of *Echinorhynchus gigas* with embryo.

[1] See the observations of von Willemoes-Suhm, *Zeitschr. f. wiss. Zool.*, Bd. xxiii., 1873, p. 343, (*Bothriocephalus*), and p. 337 (Trematoda).

[2] This holds good also for the generative buds of Gregarines—the so-called Pseudonavicellæ—which, earlier or later (in the body of their host or outside it), develop into embryos.

which are commonly said to go through no metamorphosis, the resemblance of the young to the adult is more apparent than real. In the majority of cases (in the Cestodes, Distomidæ, *Echinorhynchus*, and *Pentastomum*) the differences are so great, that there is hardly any point of similarity between the young and the fully formed worm.—(Figs. 35, 36, and 37.)

It is not so much for zoological reasons, to complete our knowledge of the organization of parasites, that these facts are brought forward, as for the reason that the heteromorphism of the embryo is of the greatest importance in their life-histories. Seeing that the structure of an animal is by no means a matter of chance, but depends upon the capacity for certain actions and modes of life, it is not surprising to find that the embryos of Entozoa, which live under different conditions from the adults, are different from them in form; and these peculiarities are all the more important, because the fate of the embryo is intimately connected with the character of its life-history.

Let us consider the actual results of observation. It appears that the history of the young parasites that have reached the exterior from the body of their host, whether as eggs or developed embryos, may follow one of two directions; either the young leave the egg and live in a free state for a longer or shorter period, or they remain within the egg until it is taken into the body of a new host, where they are then set free. In the latter case, there is no free-living stage, for it is always the eggs and not the embryos that are found at large. But it may be objected that it is impossible to draw a sharp line between a living individual and a fully developed egg. This is no doubt true; but it must be remembered that the relations between the embryos and the outer world are quite different while it is still enclosed within the egg-shell, though an embryo just hatched can hardly be said to be at a higher stage of development than a fully formed embryo still within the egg.

Whether the embryo of a parasite, when fully developed, be free or not, depends in a great measure on the character of the egg-shell. The latter, when thick and strong, imposes an increased resistance to the exit of the embryo, and sometimes renders it quite impossible for it to leave the egg by its own unaided efforts. This is effected very often by the action of the gastric juice of the new host, which dissolves the shell, or makes it so weak that the embryo can force its way out without special difficulty. My experiments [1] with the eggs of tape-worms show clearly that the hatching of the embryo is sometimes merely a question of the digestive activity of its host. In some

[1] Leuckart, "Blasenwurmer," p. 100.

cases, corresponding to the chemical and physical qualities of the egg-shell, the solvent power of the digestive juices must vary, in order to set free the enclosed embryo. The differences in the digestive activities of various animals are but slightly understood, and, in fact, are merely known to exist; but we cannot doubt that they exercise a profound influence upon the presence and distribution of parasites, when we remember that the eggs of the common tape-worm are digested by mammals, but not by frogs. It would appear that, on the whole, the digestive activity of cold-blooded is less than that of warm-blooded animals, since the larvæ of flies, wood-lice, millepedes, &c., and the shells of the eggs of tape-worms and of *Ascaris lumbricoides* are able to pass through the alimentary canal of the former without being digested. Moreover, since, as we have seen, it depends upon the character of the egg-shell whether the embryo of a parasite be hatched outside the body of its host or not, we are right in assigning to the first group eggs with thin, delicate shells; and this is especially the case in the Nematodes (*Dochmius*, *Sclerostomum*, &c.) But these thin-shelled eggs do not afford so much protection to their contents as those with a stouter shell; they are not found, therefore, in all species with free embryos, and are always absent in those cases where the time of incubation is longer. In these cases the eggs are thick-shelled, but provided at one end with a kind of lid, which yields to pressure from within, and can be raised up by the embryo (Fig. 38). These are found in the Distomidæ, *Bothriocephalus*, and in many ectoparasites, *e.g.*, the louse. But it must not be supposed that the absence of a lid of this kind hinders in every case the exit of the young; it is quite possible that the embryos are enabled, by the possession of head spines or other similar structures, to bore their way through the egg-shell, as do the young of many other animals; and in the case of *Gordius*, among Entozoa, this has been actually proved. It is also possible that a damp environment may help to soften the shell, and so facilitate the escape of the embryo, as has been observed in many thread-worms.

FIG. 38.—Eggs of *Bothriocephalus*, with operculum; the one is empty.

Be that, however, as it may, the main fact of interest to us is that there are numerous parasites which lead a free existence whilst young. The majority pass this stage in water, in localities that the egg has reached, in a more or less direct way, before the escape of their embryos. Sometimes they swim about by the help of a covering of cilia (*Bothriocephalus*, *Monostomum*, and other Trematodes—Figs. 39 and 40) or special appendages (fish-lice); sometimes they remain at the bottom, and make their way into the mud. Other species,

especially Nematodes, live in damp earth instead of water; and there are other parasites, but only air-breathing insects, that inhabit drier

Fig. 39.—Free embryo of *Distomum hepaticum.*

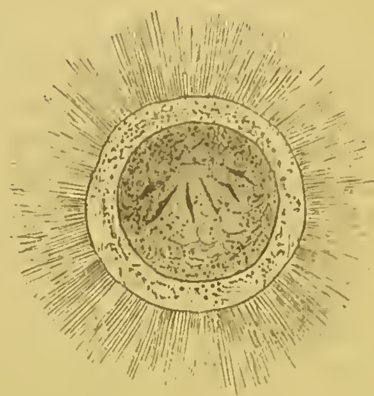


Fig. 40.—Free embryo of *Bothriocephalus latus.*

localities. As a well-known example of this, may be adduced the larva of the flea (Fig. 41), which is found in quantities in retired spots in the neighbourhood of mouldering organic matter, such as dusty corners of rooms, and in the straw of hen-houses, &c. The comparison of a flea-larva to the young of Helminths in this particular does not, however, imply that they agree in all respects. The life of a flea-larva is of long duration, and so noteworthy as regards growth and metamorphosis, that it must be considered quite as important as that of the adult. With the Entozoa, however, it is quite different,—at least with the greater number; not merely do the young (except in some cases) take no nourishment during the free stage of their existence, but the period itself is of short duration, and serves only as a means to further their distribution and migration. Instead of blind chance, which in other cases directs the fate of the germs of parasites, we have to do with a definite and fixed order of events. This free stage of existence, in spite of its short duration, is long enough, under favourable circumstances, for the parasite to make its way into the body of some host.

Fig. 41.—Larva of the flea.

In the first edition of this work I was obliged to leave it uncertain whether any parasites existed in which the free stage

was sufficiently prolonged to allow of their taking in nutriment, and so increasing in size. Regarding the manifold conditions under which the Nematoda lived, I thought it probable that examples of this kind, if they existed at all, would be discovered in this group. This opinion has been justified. My researches into the life-histories of Nematodes,[1] have proved that there are numerous species, especially among the Strongylidae (of human parasites *Dochmius duodenalis*), which in their young stage resemble in structure and habits the free-living Rhabditidæ (Figs. 42, 43), and like them go on feeding and growing for a considerable time. They then change their skin, lose the pharyngeal armature so very characteristic of *Rhabditis,* and enter upon a stage when they cease to take in nourishment and to increase in size, and need to become parasitic. I need hardly recall the life-history of *Ascaris nigrovenosa,* shortly described above (p. 2), which belongs to this type; but is peculiar, in that the *Rhabditis*-like form, which elsewhere is merely a young stage, is here developed into a special generation, which, as soon as it is completed, enters again on a parasitic life.

Among other Helminths (Cestodes, Acanthocephala, Distomidæ) there is nothing of the kind known, and it would indeed be impossible in the two first-mentioned examples, inasmuch as the young has no alimentary canal. Where there are free-living stages in these forms, they serve only for an independent migration. Moreover, the Entozoa are by no means the only animals which have a "swarm-period" like this. It has often been observed in many other animals, such as corals, ascidians, and so forth, when the adult is entirely stationary, or possesses but limited powers of locomotion. Among the insects also we know of wandering larvæ, as Newport and Fabre have shown in the Meloidæ: the larvæ of these beetles live in the nests of various species of bees, to which they can only gain access in the young condition, owing to limited powers of movement of the adults.[2]

As soon as the young parasite meets with its proper host, it abandons its previous course of life, and loses those organs which serve only to establish relations with the outer world, such as cilia, locomotor appendages, and organs of sense, when these are present,

[1] For a fuller statement see Vol. II.

[2] The life-history of these young Meloidæ is such an interesting example of pilfering, that I cannot help giving an account of it here, especially as it affords many parallels and points of relation to the study of parasitism. The females lay their eggs in early spring at the roots of the Ranunculaceæ, dandelions, and other plants rich in honey, that are much visited by bees. As soon as the larvæ are hatched, they crawl up the stems of these plants and hide themselves in the corolla. When bees visit the flowers the larvæ attach themselves to them by their powerful limbs, and are carried to the nest; here they lose their appendages and change into inactive grubs.

and in this way undergoes a metamorphosis which leads sooner or later to its definitive form. At the same time the parasite fixes

Fig. 42.—Embryo of *Rhabditis terricola.*

Fig. 43.—*Rhabditis*-like condition of young stage of *Dochmius trigonocephalus; a*, at commencement of the free life ; *b*, at the end of the free life.

itself on to the outer skin of its host, or in some organ easily accessible from the exterior. In this way we know that the larvæ of Trematodes attach themselves to the skin or within the respiratory cavities of water-snails. Others bore their way at once into the intestines or body-cavity. To attain this the parasite seeks a soft, slightly resisting part of the body, against which it presses with its anterior extremity, and gradully forces its way in. Considering the small size of the body, and the fact that many of these embryos are provided with special boring apparatus—as, for instance, the larvæ of *Bothriocephalus, Gordius,* and several species of *Distomum*—it is evident that the difficulties to be overcome are not very great, provided that they attack the right host. It is of course only animals with a delicate outer skin, such as larval Insecta, Crustacea, Mollusca, and so forth, that are attacked in this way by parasites.

In many cases the process just described has been actually observed, and in other cases it is inferred by placing together the

parasites and their hosts, and by subsequently finding the parasites within the bodies of the latter, which of course had been previously ascertained to be free from parasites. Von Siebold,[1] in the account of his researches into the Mermithidæ, and their wandering into the bodies of minute caterpillars, makes the following remarks: "Thirteen larvæ of the spindle-tree moth (*Hypomeneuta cognatella*), which I had previously found by microscopical examination to be free from thread-worms, were placed in a watch-glass, in which was a quantity of damp earth containing active embryos of *Mermis*. After eighteen hours, I was able to detect these embryos in five of the caterpillars. In a second experiment, I carefully examined thirty-three caterpillars, to see that there were no Nematode larvæ in them to start with, and placed them in similar conditions. After the lapse of twenty-four hours, fourteen of them contained embryos of *Mermis*, six of them contained two worms a piece, two others contained as many as three a piece. I also made use of young caterpillars not more than three lines in length of *Pontea cratægi*, *Liparis chrysorhœa*, *Gastropacha neustria*, which I took out of the webs in which they had hibernated. They were in a similar fashion placed in a watch-glass with damp earth and embryos of *Mermis*. On the following day I found that ten out of the fourteen contained embryos; in five there were two larvæ, and in one there were no fewer than three."

Meissner[2] has recorded similar observations upon the embryos of *Gordius*. The wandering into the bodies of larvæ of *Ephemera*, which Meissner made use of for his experiments,[3] only took place at night, and always through the appendage which served as a point of attachment for the young larvæ. "All the Ephemerid larvæ which were left for the night in a vessel with the *Gordius*-embryos were attacked by them; all the intruders, however, were found in the legs, usually in the neighbourhood of the first joint, but some had penetrated as far as the muscles of the coxa; some were quiescent, with the head and proboscis retracted, but the majority were actually moving about, and I was able to see them in the act of making their way between the muscle-bundles. This was done in a very peculiar way. The head was thrust forward, and the hooks, being directed outwards, obtained a firm hold of the tissues; the head and proboscis were then drawn back, to be again thrust forward in the same way. The proboscis thus penetrated some distance, and the hole was then enlarged by the head with its circle of hooks. The contractions of the muscles of

[1] *Entomol. Zeitung*, p. 239, 1860.

[2] *Zeitschr. f. wiss. Zool.*, Bd. vii., p. 132, 1856.

[3] Villot considers that the larvæ of *Chironomus*, and not *Ephemera*, are the proper hosts of the young *Gordius*. *Archives d. Zool. expér.*, t. iii., p. 186, 1874.

the *Ephemera* hindered this process to some extent by pushing away the *Gordius*-larvæ, and rendering their attempts ineffectual. I found one specimen in the fat body endeavouring, but without success, to make its way between two huge drops of fat: every time that the larva pushed them asunder, they flowed together again directly. The longer the Ephemerid larvæ remained in the infected water, the greater was the number of *Gordius*-embryos, which penetrated into their bodies; I found them in all the organs, the legs, palpi, fat body, and especially in the body-cavity, and even in the dorsal vessel, lying sometimes close to one of the valves, and moved to and fro by its pulsations. The number of parasites in one larva was sometimes so great (as many as forty) that I am inclined to attribute to this helminthiasis the sudden mortality which took place among the *Ephemeræ*."

For a considerable time it was believed that the parasitism of these free embryos was always brought about by their own active migration into the body of a host; of course, it was possible that it might be effected in other ways, but there was no proof of this. At present we know that many larval parasites find their way into the body of a host by means of drinking water. I transferred a quantity of muddy water containing embryos of *Dochmius trigonocephalus* (Fig. 43, *a*, *b*,) to the alimentary canal of a dog, and saw them grow into the parasite after the lapse of a few days.[1] Man is infected in a similar way by *Dochmius duodenalis*, and the horse by *Sclerostomum equinum*. It is probably only the free young stages of Nematodes which select the natural passages in order to become Entozoa; at any rate they are the only forms that can, by the thickness of their skin, withstand the action of the digestive juice. Meissner, however, and others have shown that this is not a complete protection; the former observed numerous *Gordius*-embryos destroyed by the digestive fluids of Ephemerid larvæ, and I have observed the same in *Monostomum*. In a similar fashion the often numerous specimens of *Filaria sanguinis*, which the mosquito sucks up with the blood of man, shortly perish almost without exception in its alimentary canal.[2]

[1] See Vol. II.

[2] From the observations of Manson (*Trans. Linn. Soc. Lond.*, pp. 367-8, 1884) there can no longer be any doubt that the few embryos which can pass without danger to themselves through the intestine of the mosquito undergo further development in the body-cavity, in consequence of which they now differ in size and in the structure of the mouth parts from the embryo at an earlier stage. Manson is of opinion that embryos, having thus reached a certain stage in the body-cavity, get into water only on the death of the host, and that they are taken into the human body with the water. This statement still requires demonstration, but even were this proof forthcoming, there would yet remain a possibility that the embryos evacuated with the urine (which probably no more represent a useless production than the eggs of intestinal worms which pass out with the fæces) may be transported to certain small hosts, and by these means human beings may perhaps be infected more commonly than in the way pointed out by Manson.—R. L.

A passive migration which occurs only exceptionally in Entozoa with free-living embryos is the rule in those species which have no free young stage. In the latter group the embryos, still enclosed by the egg-shell, reach in some way or other the intestine of their host; the process of alimentation affords numerous opportunities for this to happen, which may recur after intervals, varying according to the peculiarities of the mode of life.

Many animals, especially smaller ones, actually use the eggs of Entozoa as food. I have myself observed specimens of *Gammarus* and *Asellus aquaticus* feeding upon eggs of *Echinorhynchus* which I had placed in their aquarium; others again take in the eggs accidentally along with their food, in greater or less numbers, sometimes still protected by the covering of the body of their parent.

In the latter way grass-feeding ruminants are infected with the eggs of several tape-worms (*Tænia serrata, T. marginata, T. cœnurus,* and *T. echinococcus*), which live in the intestine of dogs. The "proglottides" of these worms crawl out of the fæces and deposit their eggs upon grass stalks. I may also mention here *Tænia saginata* (*mediocanellata*) of man, the eggs of which are transferred in the same

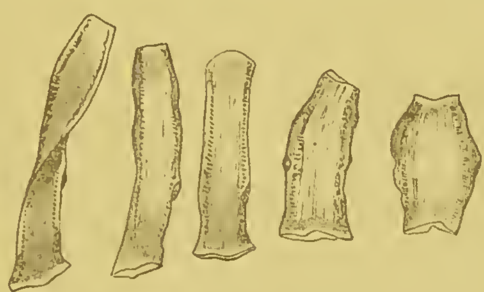


FIG. 44.—Proglottides of *Tænia saginata* in various conditions of contraction.

way to the stomach of the ox (Fig. 44); the pig generally becomes infected with *Tænia solium* by feeding directly upon human ordure, and the meal-worm (*Tenebrio molitor*) devours, along with the excrement of mice, the contained eggs of *Spiroptera murina,* while the larva of the cockchafer takes in the eggs of *Echinorhynchus gigas* with the fæces of the pig. Man himself is frequently attacked by parasites in the same way; and dogs, when licking their master's hand, deposit the eggs of *Pentastomum,* which are thus easily transferred to the alimentary canal.

These few examples show how the germs of parasites are taken in with food. In aquatic animals this is even more easily accomplished. In those that possess circlets of cilia or tentacles, the eggs may be readily swept into the mouth with food; and higher

animals, *e.g.* fishes, may be occasionally deceived, and devour tape-worms under the delusion that they are nutritious food. It is, moreover, evident that the further development of these eggs, when they have reached the body of some animal, is only possible when the conditions are favourable, and when the eggs themselves contain a living embryo. It is not easy to say how long the embryo will retain its vitality; accidental and even constant conditions bring about the greatest variations in this respect. In the eggs of the common thread-worm (*Ascaris*) I have seen active embryos even after the lapse of two or three years,[1] as also in the eggs of *Echinorhynchus;* whilst, on the contrary, the eggs of tape-worms usually lose their vitality within a few weeks, even when kept damp.

The eggs first of all, we may suppose, reach, in a living condition, the stomach of their host, where, if the digestive juices be of sufficient strength, the shell is dissolved; variations in this respect have been already alluded to (p. 58). The embryo, which was hitherto sufficiently protected by its outer cuticle against dissolution, now becomes free, and acquires the possibility of growth and development.

DEVELOPMENT OF THE GERMS AFTER MIGRATION.

That the embryos of some Entozoa, directly they are hatched, leave the stomach of their host, and find their way into its intestine, where they arrive at sexual maturity, has been placed beyond doubt. I succeeded in infecting a sheep with *Trichocephalus* by feeding it with the eggs containing embryos.[2] In a similar fashion, according to Ehlers, hens and other birds are infected with the tracheal parasite *Syngamus,* and man (according to Zenker and myself) with *Oxyuris.* Küchenmeister and Davaine attempted to breed *Ascaris lumbricoides* from eggs by drinking water containing them, but numerous and careful experiments in this direction by Mosler and myself led invariably to a negative result.

In some cases (*e.g.*, *Dochmius trigonocephalus,* as above mentioned) the free embryos also attain to maturity without change of locality. It is usual, however, for the development of the young parasites, whether hatched in the stomach or outside the body,

[1] Davaine saw embryos alive after four years, and even after five years had elapsed he was able, by heating them, to induce signs of vitality. (*Mém. Soc. Biol.*, t. iv., p. 261, 1862.) He also states that he was able to preserve alive for years eggs and embryos of *Tænia solium* and *Tænia serrata.* (*Ibid.*, t. iv., p. 273, 1862.)

[2] See Vol. II. The attempt here referred to is the first which has established the continuous development of an intestinal worm. Of course, Davaine and others had, before this, occasionally asserted such a development, but what they adduced was in no way convincing.

to follow a more complicated path. The young of *Trichina*, for example, perforate the intestinal wall, and bore their way into the surrounding organs or tissues. The same holds good for many species of *Tænia*, *Echinorhynchus*, and *Pentastomum*, whose development I have traced, and numerous thread-worms—*Spiroptera murina*, *Ascaris incisa*, *Sclerostomum equinum*, &c. If we recall and compare with these facts the additional fact that the larvæ of *Distomum*, *Bothriocephalus*, &c. bore their way from the exterior into the body of their host, and make their way into certain definite localities, we may state, in a general way, that *the embryos of Entozoa which have found their way into the body of some host do not at once become quiescent, but continue their wanderings, and traverse in various directions the tissues and organs of its body.*[1]

These wanderings are facilitated by the minute size and often elongated needle-shaped body of the parasite, or by the possession of a boring apparatus. It is, in fact, no harder for a Nematode to make its way through the tissues of an animal than for a bird to move through a thick covert, or a dog through a cornfield, and they leave as little trace of their progress, inasmuch as they rather push between than actually tear their way through the tissues.

The wanderings of parasites in the larger animals are also often assisted by their getting into the blood-vessels, and so being carried into the remotest parts of the body. Many of them even live for a time as Hematozoa, *e.g.*, the embryos of certain *Filariæ* (p. 49). In a few cases the presence of embryos of *Tænia* in the blood has been actually observed (Leuckart, Raum); in other cases it has been suspected from the wide and uniform distribution of the parasites in the body of the host. This conclusion is, however, quite a necessary one, for my researches on *Trichina* have proved that the connective tissues

[1] If such a migration take place into a pregnant female, the young Entozoa may reach the body of the embryos. Leydig (*Muller's Archiv f. Anat. u. Physiol.*, p. 227, 1851) observed in the blood of *Mustelus lævis* and its fœtus the same *Filariæ*. However, this does not seem to occur always, since in the Mammalia the transference of Nematode Hæmatozoa to the fœtus has not been demonstrated (Chaussat). The wandering embryos of *Trichina* avoid the body of the fœtus. On the other hand, I found in a pregnant *Lacerta agilis* that nearly all the embryos—nine out of twelve—contained active sexless Nematodes in the pericardial cavity, in the cavities of the brain and spinal cord, and in the amniotic fluid. Most of the embryos harboured two or three parasites, or even four, and in different parts, without showing the least traces of how the worms made their way in. In the organs of the mother I could not find any of the parasites, nor even the sexual worms which had produced them. Rathke, I find, anticipated me in this observation (*Archiv f. Naturgesch.*, Jahrg. iii., Bd. i., p. 335, 1837). The presence of Entozoa in embryos under such circumstances need excite no wonder; but the older assertions, according to which the embryos occasionally harboured sexually mature Helminths in the intestine and liver, seem most suspicious (Davaine, *loc. cit.*, p. 11).

form passages of communication from one part of the body to another, of which the embryos avail themselves.

Whether these wanderings take place through the blood-channels, through the connective tissue, or perhaps also directly through the tissues of the organs themselves, and whether they commence at one point or another, at the skin or the alimentary canal, one fact is certain, that they do not last long. *Sooner or later the embryo loses its activity, and then, if the circumstances be favourable, undergoes, by growth and metamorphosis, further development.*

These favourable conditions occur, perhaps, in only one definite organ or host—in a mammal, perhaps, or a snail, in the brain or in the liver. Here only is a further development possible. If, as is frequent, chance has brought it about that the young parasite finds its way into some other animal or some other organ, it shortly dies; but in many cases it leaves behind traces of its presence. For instance, in lambs that have been fed with embryos of *Tænia cœnurus*, which only attain to development in the brain, many other organs and tissues, such as the muscles, connective tissue, and liver, are found to be filled with minute cysts, which were no doubt at one time occupied by the worms.

The nature of the further development, of course, varies with the species of parasite and the structure of the embryo, so that increase of size appears to be the only change which can be universally predicated of parasites. Different species vary much in the dimensions which they attain; some stop short at a few millimetres in length, others only after exceeding three or four decimetres (*Ligula*).

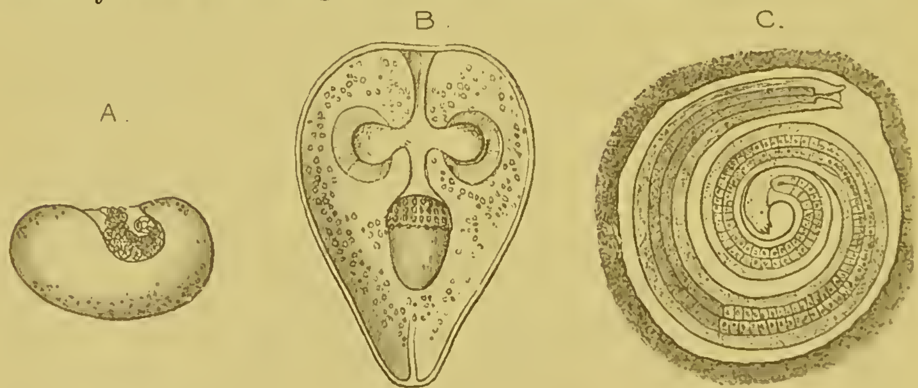


Fig. 45.—Entozoa in the second stage of development. *A.* Cysticercus of *Tænia solium* from the pig; *B.* Cysticercus of *Tænia cucumerina* from the dog-louse; *C.* Young form of *Spiroptera murina* from the meal-worm.

If the embryos differ from their parents in form, they undergo metamorphosis as well as increase of size. The organs that served

merely to assist their wanderings are cast off, and replaced by new structures, which subserve their altered conditions of life. As a general rule, Entozoa, in this second developmental stage, show a considerable likeness to the fully formed animals, but differ in various directions. The sexual organs, for instance, are incompletely developed, or even absent, so that the organization is, on the whole, less differentiated, — in accordance, certainly, with the comparatively simple and uniform conditions of life. The embryos remain quiescent, and imbedded in the tissue of organs, generally within a cyst, which, as we have seen, is formed by growth of the connective tissue, or secretion by the growing body of the parasite, and feed on the substances immediately surrounding them (Fig. 45).

Fig. 46.—A piece of liver from the rabbit, showing passages made by *Cysticercus pisiformis.*

Fig. 47.—*Archigetes Sieboldi.*

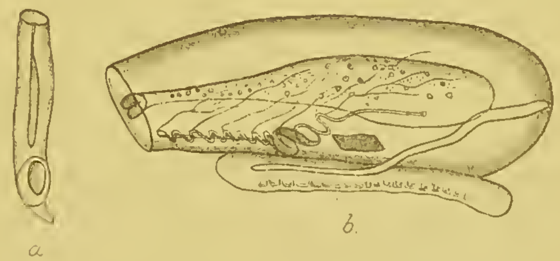


Fig. 48.—*Aspidogaster conchicola.* *a.* Embryo; *b.* Young animal, not sexually mature (after Aubert).

Occasionally, however, this state of quiescence is not absolute; the parasites move from place to place in a slow and gradual fashion, as might have been expected from the size of the parasites and the tissues that surround them. This is known to occur in certain tape-worms[1] (*Tænia cœnurus*, *T. serrata*, *T. marginata*) whose embryos develop in the brain or liver of mammals. The bladder-worms, which constitute the second developmental stage of the tape-worms, progress, so long as they remain of small size, in a definite direction by a peristaltic action, and form in this way tunnels and passages, which are subsequently invaded by a growth of connective tissue, and present a striking appearance. Sometimes these passages open into the neighbouring cavities of the body, into which the parasites then fall. This is most generally the case with the tape-worms found in the liver of rabbits and ruminants, which find their way into the body-cavity, where they again become encysted.

The quiescent stage in the life-history of parasites never takes place in the intestine, but may do so in any other organ of the body, and most generally does so in the connective tissue between the muscles and in the parenchyma of the alimentary canal; some sexually mature parasites are also found in these same organs, and hence the question arises, whether they may not be directly developed from the asexual forms, without any further migration. There are two species in which this certainly does occur; one is *Archigetes*,[2] an unsegmented tape-worm of the family Caryophyllæidæ (Fig. 47), which is a parasite in the body-cavity of many Naidæ. This worm becomes sexual while yet a bladder-worm, which, in other Cestodes, is only an intermediate stage. Another instance is furnished by the genus *Aspidogaster*,[3] which inhabits the pericardial cavity of the fresh-water mussel (Fig. 48), and attains sexual maturity without any further change of habitation.

All these creatures, however, are parasitic upon invertebrates, a fact of which the importance will appear later on. Among the internal parasites of the Vertebrata we do not know of a single analogous example. We may therefore lay down this general law, that *the quiescent stage following upon the wandering embryonic stage does not conclude the life-history of the parasite, which needs rather a radical change in its environment,—in other words, a second migration.*

[1] See Leuckart, "Blasenbandwürmer," p. 124.

[2] Leuckart, "Archigetes Sieboldi, eine geschlechtsreife Cestodenamme," *Zeitschr. f. wiss. Zool.*, Bd. xxx. (Suppl.), p. 593, 1878.

[3] Aubert, "Ueber das Wassergefässsystem, u. s. w., d. Aspidogaster conchicola," *Zeitschr. f. wiss. Zool.*, Bd. vi., p. 349, 1855.

CHANGE OF HOST—MIGRATION.

Neglecting for the present parasites that develop directly (*Trichocephalus, Oxyuris, Dochmius*, &c.), and the other two instances just

Fig. 49.—Sporocyst and Redia, with Cercariæ in the interior.

quoted, the second stage of development leads only to a certain point, which is more or less distant from the final stage of sexual maturity. But this stage lasts for a considerable time, even several years in many parasites; indeed, until a favourable opportunity affords the conditions suitable for further development. If this opportunity do not occur, they remain in the asexual state, and finally perish.

The progress of recent research has made us acquainted with the fact that these intermediate forms sometimes, of their own accord, seek out a new host, in the body of which they arrive at sexual maturity. This has been proved in the case of some marine tape-worms (*Tetrarhynchus*), and will perhaps be ultimately shown to be of more frequent occurrence. This migration is often accomplished by a brood produced asexually from the quiescent form of the second developmental stage,—it being, of course, supposed that this is active, and not, like the heads of bladder-worms, attached to the mother. This is what takes place in the Distomidæ and allied forms of Trematodes. The embryos (Fig. 49) are formed in the interior of saccular parasites, provided or unprovided with an alimentary canal (Rediæ or Sporocysts),

which thus, in conformity with the law of alternation of generations, give rise asexually to a new generation. In these cases a number of generative cells develop, which become collected together in increasing numbers, and grow into parasites which are different from the foregoing generations,[1] and are, in fact, small sexless Distomes.

In many cases this generation finds its way into the body of a host while yet contained within the Sporocyst (or Redia). In *Distomum macrostomum*, for example, whose life-history has recently been worked out by Zeller,[2] the Sporocyst (the so-called *Leucochloridium paradoxum*), having the appearance and colour of a tailed fly-maggot, is swallowed, together with its living contents, by some insectivorous bird, after having bored its way through the tentacle of the *Succinia* infested by it. About six days after, the young Distome, freed from the Sporocyst, has attained to sexual maturity, having cast off the earlier thick larval cuticle.

Such a direct transference into the definitive host is, however, rare; *it is usual for the young parasite first to enter the body of another animal.*

For this purpose, the young *Distomum* is generally provided with a tail, and often with a boring tooth at the anterior extremity. In this stage it was formerly regarded as a distinct animal, and named "*Cercaria.*" These Cercariæ (Fig. 50) abandon their host and live free for some time in water; they then seek out a new host,[3] which may belong to the Mollusca, Insecta, or Crustacea, and bore their way through its outer skin. Von Siebold[4] observed these parasites in the act of making their way into the body of their host, and he thus describes the process:—"I had obtained a quantity of *Cercaria armata* from the common pond-snail (*Lymnæus stagnalis*), and put them into a watch-glass containing a number of larvæ of Ephemeridæ and Perlidæ. I could observe, by the help of the microscope, that the Cercariæ, swimming about in the water by

Fig. 50.—A free Cercaria.

[1] Moreover, we know of cases, especially during the winter time, in which the generating cells of certain Rediæ give rise again to Rediæ. It is more generally, however, the Sporocysts that, by division or budding, give rise to a ramified structure that pierces the tissues of its host in all directions.

[2] Zeller, *Zeitschr. f. wiss. Zool.*, Bd. xxiv., p. 564, 1874.

[3] If there be no such change of hosts, the young *Distomum* has no tail. Some few possess instead a short process which looks like a sucker, and serves to assist them in creeping about.

[4] "Ueber Band- und Blasenwürmer," p. 26, "Handwörterbuch d. Physiol.," Bd. ii. p. 669, 1843.

means of the tail, approached the insect larvæ, and crept all over them in a restless fashion, evidently seeking something. I also noticed that every now and then they remained motionless, and pressed their frontal armature against the body of the larva. In no case, however, were these boring operations continued, until the Cercaria happened to have lighted upon a soft portion of the integument between the segments of the insect; then they used their spine without ceasing until they had made an aperture in the skin, through which the flexible fore-part of the body could be introduced. This enlarged the opening, and rendered it possible for the whole body, much attenuated during the process, to pass through the outer skin into the perivisceral cavity. The tail of the Cercaria always remained outside, and was no doubt detached by the sides of the aperture closing together after the body of the parasite had passed through. Having selected for these experiments young and delicate larvæ, I could still observe the Cereariæ inside their body. They invariably remained quiescent, and assumed a spherical shape (Fig. 51), surrounding themselves with a cyst. The frontal spine was detached during this process of encysting, and was generally visible, lying close to the Cercaria, and within the cyst. This spine, therefore, like the tail, is cast off as soon as its purpose is fulfilled."

FIG. 51.—An encysted Cercaria, without tail.

The duration of the free life varies with the species. In our common Cercariæ it is generally short, and many species (*Distomum hepaticum*) do not wait to make their way into the body of some host, but become encysted upon water-plants and other objects. The marine forms, on the other hand, remain longer in the free stage; some, after entering the bodies of worm-larvæ, Copepoda, &c., devour the tissues of their host, and become encysted in its empty shell (Mœbius).

In the quiescent stage the Cercariæ are just like other Entozoa in the second developmental period. They await transference to a new host, where, if circumstances favour it, they attain maturity. The changes undergone in the intermediate host—in which they sometimes remain for years—are no more than preparations for the final stage, and consist mainly in a slight increase in size, and the gradual formation of the generative organs.[1]

The change to the last developmental stage is then (even in species

[1] If this intermediate condition be prolonged to an unusual extent, the encysted *Distomum* often arrives at sexual maturity, as I have noticed myself in Ephemerid larvæ. Similar cases have been observed by other naturalists, *e.g.*, Linstow and Villot. The last mentioned has published a special paper on this circumstance ("Observ. de Distomes adultes chez les Insectes," *Bullet. Soc. Statistque de l'Isère*, t. ii., p. 9, 1868), which, however, I have not seen.

with an intercalated free-living stage) *accomplished by a passive transference,*—a process which we shall have specially to notice when the final fate of an asexual internal parasite comes to be treated of. This transference is, however, by no means always the result of a change of hosts.

In the mesenteric artery of the horse there is commonly to be found a more or less conspicuous aneurismal swelling. This is caused by parasitic Nematodes, belonging to the life-cycle of *Sclerostomum equinum* (*Strongylus equinus*), which originate from the above-mentioned (p. 61) *Rhabditis*-like embryos. The worms live in the fibrous lining of the aneurism (Fig. 52), and grow to an inch in length; they then, after casting their skin, change into the adult condition, which is characterised not merely by the development of the sexual organs, but by the possession of a conspicuous horny mouth-armature with a serrated margin.[1] Ripe sexual products are indeed sometimes absent, having been developed directly after the animal has abandoned its first habitation for the intestinal canal. This wandering, then, as has been pointed out, takes place without the parasite having to leave the body of its host. Subsequently the worm becomes detached from the lining of the aneurism, and is carried by the blood stream into the branches of the arterial system of the intestine, until their decreasing size puts a stop to further progress. Here the parasite begins to bore through the wall of the intestine, which it accomplishes by the trephine-like action of its mouth-cavity, and reaches its ultimate destination.

Fig. 52.—Worm aneurism of the horse.

But such instances are particularly rare. Whenever we have had the opportunity of observing, under similar circumstances, the transference of an Entozoon to its definitive condition, it is always accomplished by the worm—and its host—being devoured by the definitive host.[2] The importance of this for the distribution of

[1] For a detailed account see Vol. II.

[2] Occasionally the reverse is the case, as in certain tape-worms (*Ligula*, *Schistocephalus*), which are often taken up by water-fowls directly from the water (see p. 25).

Entozoa we need hardly adduce special cases to prove. The parasites are in this way handed on from one animal to another,—from an aquatic to a terrestrial animal, from a cold-blooded to a warm-blooded creature.[1] The bearer of the encysted parasite falls a prey to some more powerful foe, and is devoured by it: neither herbivorous nor carnivorous animals are secure from the invasion of parasites. The possibility of the transference of parasites increases of course with the number of animals that are devoured, and especially since the bearers of encysted parasites are usually small invertebrates. The larger animals, which need more nourishment, thus take in a gradually increasing number of parasites; and it is easy, therefore, to understand how it is that of all animals the Vertebrata are most affected by these creatures (see p. 11).

Only when the parasite has been transferred to the body of its right host, and other circumstances are favourable, does it arrive at sexual maturity; otherwise it rapidly dies. In the same way, the eggs, unless they reach the body of their proper host, die and decay.

The first change that takes place is the dissolution of the cyst, which, as in the case of the egg-shell, is accomplished by the action of the digestive juices of the stomach; the parasite then usually makes its way into the intestine. It remains for some time exposed to this action of the digestive juices, longer, perhaps, than the embryos hatched from the eggs, which, on account of their small size, can move about more freely, and also, possibly, bore into the walls of the stomach. A longer contact with the digestive juices is but rarely dangerous, since they are protected by their large size, and relatively small superficies, as well as by the thickness of the cuticle. Sometimes, how-

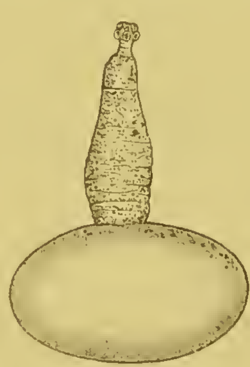


Fig. 53.—Bladder-worm with extruded head.

Fig. 54.—Bladder-worm head after digestion of the caudal bladder.

The same thing holds good for the so-called *Leucochloridium*, and its brood of Distomes (see p. 71).

[1] That temperature has an effect upon Entozoa is shown by the fact that the *Distomum* of the bat undergoes no further development during the winter sleep of its host, (van Beneden, "Les Parasites des chauves souris," *Mém. Acad. Belgique*, t. xl., p. 23, 1873). [In the same way, the Entozoa of cold-blooded animals, when they have not arrived at maturity, stop their metamorphosis during the winter, and produce no eggs, or only very few; and also, under similar circumstances, Rediæ, instead of producing Cercariæ, give rise to new Rediæ.—R. L.]

ever, this is not the case, as in the so-called "caudal" bladder of bladder-worms (Figs. 53 and 54), which has a large surface and comparatively thin walls. This bladder is frequently dissolved,[1] so that the only part which reaches the intestine of the host is the head, which is the most important part of the bladder-worm. There is also no doubt that the varying digestive power of the juices exercises a considerable influence on the fate of these parasites, just as we saw that it did upon the young individuals hatched from the egg in the alimentary tract of their host (p. 59). If the action of the digestive juice be not strong enough, as in the case of the frog, which is incapable of dissolving the cysts of *Trichina*, or if it be too strong, and therefore destroys the parasite as well as its cyst, there is evidently an end to the life of the intruder. In these cases the host is not the proper host, for it does not afford conditions suitable for further development.[2]

Besides the action of the digestive juices, there are other important factors to be taken into consideration. In the Trematodes, for instance,—at least, in those that perform their migration as free larvæ (p. 72),—the presence of a capsule is necessary to further development (de la Valette), but not in *Tænia*, perhaps because the former, in consequence of their small size and delicate covering, require some protection against the action of the digestive juices of the host. The nutrition required by the parasites themselves is variable in a still higher degree; but we will return to this point later.

These processes that I have briefly noticed in the foregoing pages have been proved experimentally step by step. In this way we know that bladder-worms and muscle-*Trichinæ* arrive at maturity in the intestine of their proper host, and that the *Echinorhynchus*-embryos of our common *Gammarus* and *Asellus* become adult in fish (*Echinorhynchus proteus*) and water-birds (*Echinorhynchus polymorphus*). Thus also the encysted Nematode of the meal-worm (Fig. 45, *C.*) has been shown to develop in the stomach of the mouse into *Spiroptera murina* (*vel obtusa*), and *Distomum echinatum* of the pond-snail (*Paludina*) to acquire sexual organs in the bodies of ducks.

The life-history already quoted (p. 49) of *Filaria sanguinolenta* renders it probable that the sexually adult parenchyma-worms also

[1] In another place I have experimentally shown that the same alteration takes place outside the body of an animal, "Blasenbandwürmer," p. 156.

[2] The first changes often go on in the "wrong" host, and in experiments by the aid of artificial digestion, as well as in the proper host. The Cysticercus of the pig, for instance, when introduced into the alimentary canal of the dog and rabbit, becomes on the following day a free tape-worm head, just as if it were in the human alimentary canal; but it does not develop any further, and soon dies.

are developed from younger stages that are also internal parasites. *Filaria Medinensis* has been shown by Fedschenko[1] to make its way into its host as a larva concealed in the body of a *Cyclops*, which is swallowed along with the water in which it lives. The young worms then reach the intestine, where they remain but a short time, and then bore their way out. The analogy of *Filaria sanguinolenta*, which is often met with in a larval condition in the so-called "worm-knots," suggests this, and also the consideration that the difficulties of further internal wandering increase with the growth of the worm. It is no doubt a fact that large, full-grown thread-worms and *Tæniæ* do bore through the alimentary canal, and even the body-wall of their host; but this is rare, and when it does occur, the progress of the worms is no doubt assisted by pathological conditions set up in the tissues by their boring. These facts have no special importance in the life-history of parasites, and are rather to be looked upon as accidental, often indeed seriously affecting the life of the host.

It does not at all follow that every Entozoon that lives outside the alimentary canal must necessarily pass through the latter to reach its desired locality; Nature has many ways of achieving her ends. An instance of this is afforded by *Pentastomum tænioides*, which has a life-history like that of a typical Entozoon. The young form (formerly described as a distinct species, *Pentastomum denticulatum*—Fig. 56) inhabits cysts in the liver and lung (Fig. 55) of herbivorous mammals; presently the young animal breaks through its cyst, and makes its way into the body-cavity, after causing considerable injury to the tissues during its transit, and occasionally even causing the death of its host. Sometimes it wanders again into the viscera, most frequently the lymphatic glands. If the body of its host be devoured by a dog or some carnivorous animal, the young *Pentastomum*, if not already encysted, finds its way directly through the nostrils (and perhaps also the posterior nares) into the olfactory cavity, where it attains sexual maturity.

This habit of active migration accounts for the presence of special organs of locomotion, hooks and spines (Fig. 56), which are developed towards the close of the resting stage, and finally laid aside after they have served their purpose. If the young *Pentastomum* left of its own accord the body of its host, and sought out no fresh host, it would be an example of a periodic parasite attaining sexual maturity while leading a free life. That there are parasites with a life-history of this kind, was briefly stated at the commencement of this chapter; they are mainly insects, especially flies and wasps. The

[1] See Vol. II.

Gordiaceæ and Mermithidæ are instances of this kind of parasitism among the Entozoa, and the migration from the body of their host of

Fig. 55.—Lung of rabbit infected with Pentastomida.

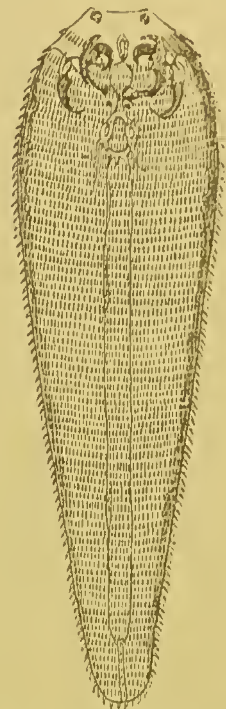


Fig. 56.—*Pentastomum denticulatum.*

proglottides and other sexual Helminths (*e.g.*, *Oxyuris vermicularis*) presents an approximation to the same phenomenon.

The young of these periodic parasites, at least in the case of insects, show certain peculiarities induced by the fact that their migration into the body of a host is accomplished for them by their parents. The latter, possessing as they do the power of free locomotion, can evidently influence considerably the fate of their eggs, which is quite as evidently impossible to the Entozoa. Thus the gad-flies lay their eggs on the hair of certain mammals, in situations whence the young can easily in an active or passive manner (*e.g.*, by being licked up) reach their next destination. The Ichneumonidæ make matters easier still for their descendants, by depositing their eggs directly in the perivisceral cavity of caterpillars, for which purpose they are provided with a suitably constructed boring ovipositor.

The converse of this is illustrated in the Gordiaceæ and Mermithidæ, whose eggs are laid in water or damp earth, and the young when hatched find their own way by active migration into their proper host, as has already been said. Whether the embryo be conveyed passively or actively, it makes its way into the body of its host, and becomes in

the interior of the infected animal (sometimes even in the intestine, *e.g.*, *Gastrus equi*) a parasite which may be compared to the second developmental stage of a Helminth. Though there is but rarely an actual encystation (even in the Helminths this condition is sometimes absent), the parasite usually remains quiescent for a time, which it spends in growth and preparation for its future metamorphosis. At the end of this period, it instinctively begins to travel, and leaves its place either by the natural passages (the gad-fly of the horse, for instance, through the anus, that of the sheep through the nasal cavities), or if this be impossible, by boring through the tissues; the parasite thus arrives at sexual maturity at large, and often differs markedly in form from the preceding larval stage.

This wandering often causes the death of the host when it is only a small animal, which is hardly surprising, considering the relative size of the parasite and the injuries it must cause by making its way out. In *Gordius* the life-history is more complicated, inasmuch as this parasite passes into a second host before commencing its metamorphosis. There are some facts which show that this is not peculiar to *Gordius*, and that certain other Nematodes have in all probability a similar life-history.[1] It is evident that, in spite of apparent differences, the parasitism of *Gordius* is fundamentally similar to the cases already mentioned, and may without any difficulty be classed with them. In both cases there are three life periods, generally distinguished by a difference in form—the embryo, the sexually mature adult, and an intermediate stage, which, in view of its outward characters, may be termed a "pupal" stage, if the use of this word will not bring us into a hazardous conflict with the customary terminology when we come to treat of the larvæ of parasitic insects. Each of these three stages represents in its biological relations a special department of life. The embryo is destined to commence the parasitism; it migrates, while the "pupa" resumes the prematurely broken development, and carries it on so far that, after passing to the third stage, sexual maturity appears. The migration, which is the cause of this transitional condition, is usually passive, requires no special advances in structure, and is not effected by any particular developmental conditions.

This is, of course, merely a rough sketch of the life-history of parasites, and may be regarded as a generalised description, subject, therefore, to manifold variations in the way of either greater complexity or greater simplification. Complications arise, for example, by the introduction of an intermediate generation with independent migrations. On the other hand, the life-history may be simplified by the inter-

[1] For details see Vol. II.

mediate stage passing directly, and without migration, into the sexual condition.

All this, however, is quite exceptional, and the rule for the life-history of parasites may be stated as follows:—*The life-history of parasites is divided into two stages*—(1) *the larval, and* (2) *the sexually mature adult; and each of these is passed in the body of a separate host.* Sometimes these two hosts may be merely two individuals of the same species, as in the case of *Trichina;* but generally they are quite different, and may belong even to separate orders or classes. *Tænia crassicollis* inhabits the liver of the mouse while in the young condition, and the intestine of the cat when adult; *Tænia marginata*, the connective tissue of sheep and oxen when young, and finally the intestine of wolves and dogs; the adult *Tænia solium* of man is found in the young condition in swine. In a similar way the life of *Ligula* is divided between fish (Cyprinidæ) and water-birds; of *Echinobothrium typus*, between rays and Gammarina; of *Distomum echinatum*, between ducks and *Paludinæ;* of *Amphistomum subclavatum*, between the frog and *Planorbis;* of *Pentastomum tænioides*, between the dog and rabbit, and so forth. These examples do not merely prove the justice of the general principle just enunciated, but also bring out prominently the fact that the host of the young parasite is frequently an animal which serves as food for the definitive host; thus the mouse yields to the cat not only its flesh, but its parasites, and the like happens with the rabbit and dog, the fish and the sea-gull. And this fact is not difficult to understand from a physiological as well as a teleological point of view. If one animal select as its food a certain other animal, it evidently follows that the latter is best suited to its nutritive requirements, hence the conditions of nutrition in both must be somewhat similar, and a parasite capable of living in one would probably also find the other in a great measure favourable to the conditions of its life. This idea, however, must not be pushed too far, since we find, for example, the young of *Tænia crassicollis* in many animals which are not preyed upon by cats; so also the human tape-worm is occasionally found in the asexual state in man himself,—a fact which, on the principles just enunciated, would seem to justify cannibalism from the stand-point of natural history. The presence of the young stages in Carnivora is certainly to be looked upon in the above light. The Herbivora also often contain parasites which live in the young stage in bodies of other animals;[1] but in these cases, the latter inhabit the same

[1] The statement of Von Siebold ("Handwörterbuch d. Physiol.," Bd. ii., p. 647), repeated recently by Ercolani, that the Herbivora become infected with their parasites through the medium of their food, because the parasitic Nematodes of many plants develop in their bodies, has no foundation. The Nematodes of plants are independent species, which are never parasitic upon animals. [On the other hand, the recent researches of

localities, and have been probably swallowed accidentally along with the food.

Local conditions also are of great importance in the distribution of parasites, as has been shown by Melnikoff and myself,[1] in the case of the dog-louse (*Trichodectes*), which harbours the young of *Tænia elliptica* (Fig. 45, *B*) and passes it into the dog.

Although the life-histories of parasites largely depend, in the most varied manner, upon the mutual relations of the animals that are their hosts, it is also true that chance plays a very large part in their determination. It is quite by chance, for example, that the egg meets with its proper host, or that its host is subsequently devoured by some other suitable animal. The more complicated, in fact, does the life-history of the parasite become, the greater risk does it run of not being able to complete its life-cycle. Millions of germs perish for one that reaches maturity.[2] We have, however, already spoken of this, and shown how it is compensated by the immense fertility of parasitic worms. "If the eggs and embryos of Helminths always attained to a suitable environment, the bodies of all men would be absolutely full of tape-worms, Nematodes, and other parasites." And it need hardly be pointed out that the lives of the parasites, as well as of their hosts, would be greatly endangered by this. The complicated life-history of the parasites serves as a means of checking their too rapid increase, and their metamorphoses and migrations, therefore, are of the highest benefit to them.

Von Siebold has considered that those Entozoa found in the bodies of the wrong hosts have "lost their way."[3] Nothing can be said against this simple statement, but the conclusions which he has drawn from it are by no means correct.

In the first place, it must be remembered that any animal which has wandered into a locality where its proper food cannot be obtained—a stranded whale, for instance—may be said to have "lost its way." The expression ought not to be confined to parasites, although perhaps the occurrence is more general with them. Weinland speaks in the following way of the life-history of corals:[1]—"During the breeding

Thomas and myself render it very probable that ruminants and other herbivorous mammals devour *Distomum hepaticum* along with plants, to which Cercariæ are attached in the encysted state.—R. L.]

[1] *Archiv f. Naturgesch.*, Jahrg. xxxv., Bd. i., p. 62, 1869. See also Vol. II.

[2] A tape-worm has an average life of two years. It produces in this time some 1500 segments (see p. 43, note), each containing 53,000 eggs, the total number of eggs being therefore about 85,000,000; since the number of tape-worms remains about the same, one only of these 85,000,000 of eggs reaches maturity. The probability, therefore, against each tape-worm arriving at maturity is as 85,000,000 to 1.

[3] "Handwörterbuch. d. Physiol.," Bd. ii., p. 650.

season of the coral polyps, myriads of microscopic embryos swarm in the neighbourhood of the parent stock; millions of these are washed out to sea and on to dry land, and perish, or fix themselves in positions where they cannot grow; but if only a single one find a spot suitable to its growth, Nature has accomplished her purpose, and if this one have reached a spot, perhaps hundreds of miles away, where no corals previously existed, it founds a new colony, which possibly, after the lapse of time, rises as an island out of the sea. These embryos attach themselves to any firm point, but there is no instinct leading them to select a favourable place; Nature, therefore, produces them in such countless numbers, that, on the theory of probability, some are certain to obtain a suitable locality."[1] Who would deny that this is precisely analogous to Helminths "losing their way?"

Moreover, von Siebold does not say of those Helminths that they have wandered into the wrong host, but into the body of some animal "not appointed to be their host." But this expression has really no definite meaning. If a parasite develop in any given locality, we may conclude that it finds there the necessary conditions of existence; if it do not develop, we may likewise conclude that the conditions are unfavourable; but who would undertake to decide whether or no a particular host were "appointed?" Von Siebold, however, goes still further; he states that these parasites which have lost their way do not usually die, but continue to grow, "though, on account of the unfavourable environment, they do not thrive, and fail to attain sexual maturity," and in fact "degenerate."[2] Von Siebold maintained this opinion,[3] even after Küchenmeister had endeavoured experimentally to contradict it;[4] indeed his words at Königsberg in 1860 show that he was then still convinced of the accuracy of his opinion:—"I cannot understand why the possibility of degeneration in worms is not admitted, since the same thing has been shown to take place in higher animals, as a result of unusual conditions of climate and changed food, and is regarded as a cause of the formation of new species. If in many races an extraordinary growth of hair take place, in some ruminants the horns become larger, the ears of certain domestic animals become larger and droop, and in others again a local deposition of fat takes place; why is it not possible that in many lower animals the influence of varying conditions of the body may give rise to the presence of a serous fluid in certain parts, a local dropsy?"[5]

[1] *Jahresh. d. Ver. vaterl. Naturkunde Württemberg*, Bd. xvi., p. 31, 1860.
[2] *Loc. cit.*
[3] "Ueber Band- und Blasenwürmer, u. s. w.," p. 65. : Leipzig, 1854.
[4] *Prager med. Vierteljahrschrift*, Jahrg. ix., p. 106, 1852; "Ueber die Cestoden im Allgemeinen, u. s. w.," p. 12: Zittau, 1853.
[5] "Königsberg Naturf. Versamml.," 1860.

These last words show that the author regarded the asexual bladder-worms as Helminths that had degenerated and become dropsical, in consequence of having lost their way, and got into the body-cavity or muscles of their host instead of its intestine.

Bladder-worms (Fig. 57) and encysted *Trichinæ* (at that time only known in the encysted condition—Fig. 58) were the only parasites regarded thus by von Siebold, and at that period neither the importance nor wide distribution of the encysted condition in the life-history of parasites was understood, the generally received opinion being

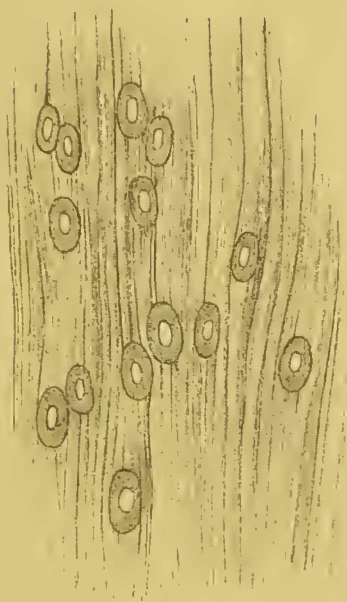


Fig. 57. Measly port (natural size).

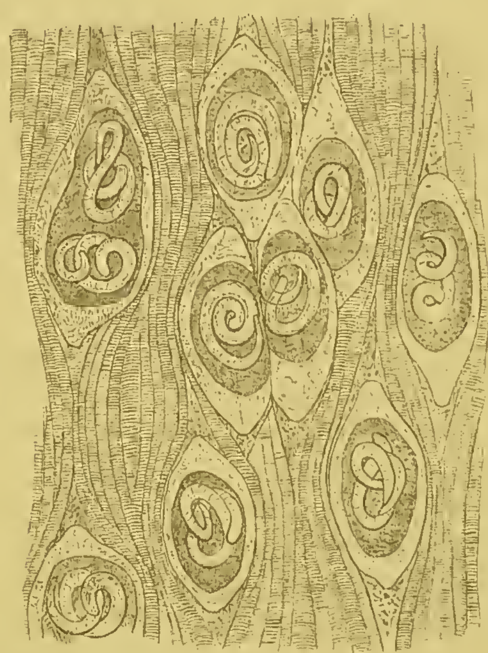


Fig. 58. Trichinosed pork (enlarged 45 times).

that the germs migrated immediately into the body of their definitive host. At this period, then, von Siebold's hypothesis was an attempt to explain certain striking and unintelligible facts, but has now become out of date. It is just these bladder-worms and *Trichinæ* that have become by a remarkable concurrence of circumstances the very subject of experimental investigation, and we are now thoroughly acquainted with their natural history. There is not the slightest doubt that what von Siebold considered to be abnormal conditions are in reality the ordinary stages of development; that *Trichina*, before arriving at sexual maturity, always passes through a stage in which it is encysted in muscle, and that in the same way tape-worms are invariably derived from bladder-worms. We can, therefore, lay aside von Siebold's theory, which has now hardly any supporters, in spite of the great reputation of its originator.

Our remarks, moreover, are only directed against the practical application of the degeneration theory, and not to an equal extent against its theoretical truth. Degeneration *per se* is quite as possible among Helminths as any malformation, which is the result of an unusual or insufficient combination of the causes of development. In this way are to be regarded certain varieties in the form of Helminths, as, for example, the so-called *Echinococcus multilocularis* or *Cysticercus racemosus*[1] (Fig. 59), considered even quite recently to be "degenerated" (that is to say, pathologically altered) forms. We are, therefore, in principle brought back to von Siebold's standpoint, or even to that of Pallas (1767) and Hartmann (1685), who were the forerunners of von Siebold in this theory,[2] but, nevertheless, we cannot agree with the applications of that theory, and the conclusions that were drawn from it.

FIG. 59.—*Cysticercus racemosus* (after von Siebold).

This matter, which has been briefly touched upon, leads us naturally to an inquiry into the conditions of development among Helminths, or, in other words, *the influence which the environment exercises upon their development.*

An Entozoon, as we know, only develops when its host can fulfil its needs. What happens, then, if it cannot? It has been already said that a parasite under these circumstances perishes; but the conditions which give rise to this decay, and the time that it takes, are subject to great variations. In the next place, we may mention that the conditions which render development possible are remarkably restricted, so that circumstances of the most varied kind come into play. It is, for example, a well-known fact that the famous Cœnurus only develops in lambs. It has been proved experimentally that the older the lamb becomes the more difficult it is to rear the worms in its body. After feeding the animal with the young parasites, it can be stated with almost mathematical accuracy when it will begin to show the effects of the infection; while it can be stated with the same probability that an older sheep will continue in good health though infected with an equal number of parasites. These facts are not peculiar to Cœnurus, but common among bladder-worms, though

[1] See for a description of this peculiar form Heller in Ziemssen's "Handb. d. sp. Path. u. Ther.," Bd. iii., p. 334 (Eng. transl., "Cyclop. Pract. Med.," vol. iii., p. 598, London, 1875), and Marchand, *Virchow's Archiv f. pathol. Anat.*, Bd. lxxv., p. 104, 1879. Numerous other observations have been made on the frequently irregular forms of the bladder-worm of the brain in man by von Siebold, Krabbe, and others.

[2] See the historical introduction in my "Blasenbandwürmer," pp. 11-13: Giessen, 1856.

the immunity from their attacks enjoyed by older animals is not perhaps so strikingly shown as in this case.

Nothing is known of the reason of these phenomena. It is quite uncertain whether it be the nutritive conditions that influence the parasite, or perhaps the greater readiness with which the young tissues yield a path for its wandering. It is not, however, age alone which limits the conditions of this individual development, for we may observe, although rarely, even among old sheep, fresh cases of staggers; whereas, on the other hand, among lambs we may find single instances of complete immunity from these parasites. Thus, for instance, Baillet mentions the case of a lamb which was fed with mature segments of *Tænia cœnurus* nineteen times in the course of about eight weeks, and still no Cœnurus was developed.[1] The experimental helminthologist has often, and even under similar conditions, to register most unexpected results. Thus the author had fed a dog with a multiple-headed Cœnurus, and in about ten days the intestine was filled with more than a hundred completely developed tape-worms; while in another similar experiment, after three weeks there were found in the intestine of the dog only heads of tape-worms, with bands of segments an inch long attached to them in a few cases only; and in a third experiment a decidedly negative result was obtained. These three cases are, of course, exceptions, for we may accept it as a rule that the Cœnurus-heads develop completely within three weeks into sexually mature tape-worms. Usually, however, even after this time one may find single immature tape-worms, sometimes even here and there an isolated head; but these are irregularities which depend rather upon the parasite than upon the host. Analogous cases are also observed in other helminthological experiments.

Just as old sheep cannot be infected by means of the embryos of *Tænia cœnurus*, so in a similar manner muscle-*Trichinæ* develop only rarely in dogs, even though the embryos are found to wander in masses from the intestines into the body-cavity. Similarly Pagenstecher and I were unable to obtain muscle-*Trichinæ* in birds, although thousands of pregnant animals lived in the intestine. In pigeons the introduced worms never reached sexual maturity. They grew and became similar in appearance to mature animals, but the sexual organs remained without germinal substance (Leuckart).

From these instances, it is apparent that the conditions of development of parasites are circumscribed—that is to say, besides the "right"

[1] *Ann. Sci. Nat.*, sér. 4, t. x., p. 190, 1858. In a similar manner Fiedler ("Zur Trichinenlehre," *Deutsches Archiv für klinische Medicin*, Bd. i., p. 68, 1865) reports the case of a man who ate a piece of raw meat, which was strongly infected with *Trichinæ*, without suffering from it.

and "wrong" hosts, there are also hosts which only partially satisfy the needs of parasites. In such hosts the invading parasites do not perish immediately after their introduction; on the contrary, they begin to develop as usual, and continue to do so up to a definite point, without, however, completing their development. Whether the worms continue for a longer time in this immature condition, or whether they perish earlier, will apparently depend upon the degree to which the conditions of development influence the life of the parasite. These may vary in individual cases.

Moreover, the above-mentioned phenomenon may be confirmed by other examples. If a rabbit be fed with the bladder-worms of the common tape-worm of the dog, they not only undergo the usual changes during their sojourn in the stomach (as has been already observed above (p. 75) with regard to the bladder-worms of the pig originating from *Tænia solium*), but they also delay for some time in the small intestine, fastening themselves to the intestinal wall just as in ordinary cases. Some of them even develop a short segmented chain, which differs from the normal beginning of the body of the tape-worm only in that its segmentation is less complete. But here the development stops, until after about ten to twelve days the young worms have all perished (von Siebold, Küchenmeister). A similar result is obtained by feeding with *Tænia cœnurus*. Since the bladder-worm of this tape-worm usually develops only in the brain of lambs, one would expect that the embryo would migrate only thither. But this is not the case, as has been already mentioned (p. 67). The embryos scatter hither and thither from the alimentary apparatus into the diverse organs of the host; but everywhere, with the exception of the brain, they perish very soon after their entrance. If the infected lamb be examined about three weeks after the feeding, one finds, besides a number of small rounded bladders situated in the brain, which are the first beginnings of the future Cœnurus, also numerous white knots, having the appearance of tubercles, which are situated in the liver and lungs, and more especially between the muscles, and upon closer examination can be recognised as cysts, which have developed round the embryos. Sometimes these cysts may contain the young of the invading tape-worm—small, more or less opaque, and shrunken bladders—more rarely they are unchanged and alive, like those in the brain, although for the most part less in size.[1] In rare cases one of these small bladders may develop in time into a complete Cœnurus.[2]

[1] See on this head, and on the development of Cœnurus in general, Haubner, *Gurlt's Magazin für pathol. Anat.*, pp. 248 and 375, 1854.

[2] Thus Eichler found a developed Cœnurus under the skin of the sheep, Nathusius under the skin of an ox. Also in the rabbit the Cœnurus has been observed in the peripheral organs, but never as yet in the brain.

The causes of these diversities are not yet known to us. We cannot even explain why the liver or the intermuscular connective-tissue has a different influence upon the development of the brood from that of the brain. The supposition that the cause lies in certain differences in the supply and quality of the nutrition cannot of course satisfy us.

Here and there, however, the space afforded by the different organs, and the peculiarities in the anatomical arrangement of the tissues, may influence the development of the parasites. In this way the bladder-worm in the brain of man grows in the subarachnoid space into sinuous strings, dilated here and there into vesicles, which may reach a length of 25 cm., but only rarely develop a head, so that the true nature of this formation (the above-mentioned *Cysticercus racemosus*) has only recently been recognised. Also the so-called "multilocular" *Echinococcus* is perhaps only due to the position it occupies in the body; whilst, on the other hand, the sterile *Echinococcus* (Acephalocyst) and the hydatid—two other forms which can scarcely be considered as normal—point to conditions of development which have to be sought in another direction.

There are only few animals in which the metamorphoses and their individual phases are dependent upon the influence of external factors to such a degree and in such an evident manner as is the case with the Entozoa. The young parasite, if the opportunity of migrating to its definitive host be wanting, remains stationary for life at a stage of its development, which its more fortunate associates, and perhaps even their descendants, have long ago left behind them.

Moreover, it is not only the periods of migration and development which cause Helminths to be dependent on external circumstances to such an unusual degree. In their later period of existence also their independence is only a limited one. All the different disturbing influences which attack the host, and endanger its health and existence, have more or less an indirect influence upon the indwelling parasite. Some may by certain steps be expelled from the intestine and other internal organs,[1] whilst others may perish through the inflammatory condition of their dwelling. For this reason also it is difficult to determine with certainty the *natural length of life* of parasites. Concerning some, of course, we know that they continue to live in exposed situations, not only for several years, but even through a whole decade (*Bothriocephalus latus, Tænia saginata*); but others again scarcely live longer than a few weeks. On the whole, the period of existence of Entozoa may be assumed to be longer than that of free-living animals of a similar size.

[1] Thread-worms often forsake the intestine on the occurrence of diarrhœa.

This is especially true with regard to immature encysted forms, which often live for several decades. With regard to *Echinococci* and muscle-*Trichinæ*, it is well known that in some instances they have lived over twenty years, whilst their corresponding sexual forms perish in a few weeks.

The changes undergone by those Entozoa that die in their host, and remain there, differ according to circumstances. Some pass through the process of mummification, others that of fatty degeneration, and others again calcify.

CHAPTER V.

THE ORIGIN OF PARASITES,

AND THE GRADUAL DEVELOPMENT OF PARASITIC LIFE.

If we endeavour to summarise our knowledge of parasitic life as we have delineated it above, and to express its principal modifications in a few words, we shall arrive at some such scheme as the following:

I. *Temporary Parasitism.*—To this category belong almost exclusively ectoparasites, which differ from their free-living relations in respect only of the quality and source of their nutriment.

II. *Stationary Ectoparasitism.*—The animals in this group show, on the whole, only slight peculiarities. They either pass through all their developmental stages (from the egg onwards) on the host, or at first lead an independent existence under a form more or less different from the adult.

III. *Entoparasitism.*—The entoparasite is always stationary, but, with the exception of *Rhabditis*, which is apparently only occasionally parasitic, never passes through all its developmental stages in one host. The young brood is expelled, either in the form of free embryos or of more or less developed (perhaps wholly undeveloped) eggs. In the latter case the embryonic development occurs in the free state. But from this stage onwards the fate of the embryos varies in different directions.

(1.) The embryos of Entozoa lead a free life for some time under an altered form (Nematodes, with *Rhabditis*-like young stages). They are not only capable of free motion, but take in food just in the same way as other creatures.

(*a.*) In the course of this free life the young form arrives at sexual maturity, and thus only the sexually produced descendants return again to parasitism (*Rhabdonema* (*Ascaris*) *nigrovenosa*).[1]

(*b.*) The young form itself becomes again a sexually mature parasite at a certain stage of its development. From the commencement it enters its definitive host, and its development ends there, although this happens occasionally, as in the case of

[1] Since the name *Ascaris* is quite incorrect to apply to these animals, I shall adopt henceforth the new generic name *Rhabdonema* to designate them.

Sclerostomum equinum, in a provisional situation. To the former class, among others, belong certain Strongylidæ.

(2.) The embryos find, in pursuance of an active or passive migration —without ever having led a free life—an intermediate host, in the organs of which they develop into a larval form, which then ends its life-history under various circumstances.[1]

(*a.*) The larva migrates, and becomes, after complete metamorphosis, a free-living animal (Oestridæ among other flies, Ichneumonidæ, Mermithidæ, Gordiaceæ.)

(*b.*) The larva arrives at sexual maturity in its intermediate host without further metamorphosis, as in the above-mentioned *Archigetes* and *Aspidogaster* (p. 69).

(*c.*) The larva remains in the intermediate host until it migrates into its definitive host, mostly in a passive way (with food). The developmental history in such cases is extended over two different hosts. This is the form of life-history which we discover in the majority of intestinal worms, and may be considered as really typical among Entozoa (Cestodes, with the exception of *Archigetes*, Acanthocephala, Distomidæ, and Pentastomidæ). In individual cases there are here certain modifications, thus—

(*α.*) The number of intermediate hosts increases, whilst the larva either migrates of itself, and seeks a new host (certain Cestodes), or produces asexually a new generation, which then enters upon a similar change of host (Distomidæ).

(*β.*) The intermediate and definitive hosts become one and the same when the embryos do not forsake the latter, but simply wander into its peripheral organs, and there develop into larvæ (*Trichina*).

(3.) The embryos pass at once, whilst they are yet enclosed by the egg-shell, in a passive manner into the intestine of their definitive host, and here complete their further development. To this class belong numerous Nematodes, especially *Trichocephalus* and *Oxyuris*.

The order in which we have drawn up the various modifications of parasitic life affords us at the same time a picture of the gradual increase in development of which this life is capable. The first

[1] The form of entoparasitic life which is here shortly characterised is that which was earliest known to us, and when the first edition of this work appeared, it was the only one known. The existence of the other forms (1 *a.* and *b.*, and 3) has only been proved later through my researches, especially with regard to Nematodes. (See Vol. II.) To these Helminths, which develop according to the newly discovered laws, belong the most important human parasites; and yet Küchenmeister ("Parasiten," 2d Ed., Preface) maintains that to the knowledge of parasites "nothing new or of practical importance can be added" beyond what he had asserted!

beginnings are lost, as has been remarked above (p. 1), in the phenomena of ordinary life, which latter evidently forms the starting-point of parasitism, or in other words, *parasites have, by accommodating themselves to the conditions of a parasitic life, in course of time sprung from creatures originally free.*

The mode of origin which we thus assert for these creatures is in principle precisely the same as that which we also assert, in consonance with the doctrine of descent, for the individual free-living forms, when we maintain their development to have been brought about by means of various influences, either directly from one and another, or from a common original form. The manner of adaptation is of course different, inasmuch as in the case of free-living animals there is usually a development of faculties which bring about a more extended and complicated capacity, whereas parasites, on the contrary, have a correspondingly limited relationship to the outer world, according to the degree of their parasitism. It is only under the influence of ever-changing surroundings, and in the full enjoyment of unembarrassed activity, that an organism can develop itself in every respect and fully form its capacities. Limitation of function is succeeded by stunted growth, and this it is which gives to parasites—at least to stationary parasites—their peculiar features. The organs and arrangements which serve to act upon the outer world, and are excited by it, disappear under the influence of a confined existence; and by thorough-going parasites this is the case often to such a degree, that the whole organism, which at other times is so artistically formed, degenerates into a simple tube, whose capabilities are almost entirely expended in nutrition and generation.[1]

These influences of parasitic life are especially apparent in those forms, the near relations of which lead a life either completely, or at least to a great extent, free. The classical researches of Johann Müller[2] have made us acquainted with a Mollusc (*Entoconcha mirabilis*) which, in its young form, possesses the usual attributes of these animals, and does not differ from related young forms any more than the latter do from each other; it lives also, for a time, in the ordinary free state,

[1] This view had already been advocated previously to the rise of the Darwinian theory. In the case of Epizoa by Nitzsch (*Magazin der Entomologie*, Bd. iii., p. 261, 1818), and for Entozoa by my uncle Fr. S. Leuckart ("Versuch einer naturgemässen Eintheilung der Helminthen:" Heidelberg, 1827). The latter says (*loc. cit.* p. 10), "The Helminths show a manifold relationship and likeness to other orders and classes, but at the same time present important differences from the related forms of animals, which, without doubt, have their origin in the entirely different mode of life of the parasitic worms, and in their circumscribed and completely isolated abode."

[2] J. Müller, "Ueber Synapta digitata und die Enstehung von Schnecken in Holothurien:" Berlin, 1852.

but ultimately becomes parasitic,[1] at the same time losing not only its shell—which is also the case with certain other snails—but also its locomotor, sensory, and alimentary organs, and degenerates into a simple sac filled with sexual products. In the form of this "snail-sac" the parasite is found in the body-cavity of the vermiform Holothurian (*Synapta digitata*), having its thickened knob-like anterior extremity inserted into the intestinal vessel of its host, so that it may easily be mistaken for a true organ of the latter. No one, without knowledge of the young form, could recognise its Molluscan nature.

If we regard this retrograde development as a consequence of parasitism, we do not thereby mean to imply that this exerts its influence from the commencement, and with full force in each individual animal, and that the same process is repeated *de novo* each time in a similar manner. The influence which the external relations of life exert upon the development of an organism in the present case, as everywhere else, can only have been a gradual one, which must have continued to work for many generations before it could produce such extreme effects. It is not a sudden transformation, but a slow and steady progressive adaptation to the conditions of a parasitic mode of life, of which we see the results in the above-cited organism. We must accept the conclusion that the Mollusc—to continue with our example—has not exhibited this particular form of parasitism from the commencement, but has only gradually adopted the above-described mode of life.

When the number of parasites in any group of animals is increasing, we often see also the various stages of parasitism in existing forms allied to each other. The sum of the degeneration and transformation is then seen to be of different extent in different species, for the transformation of the organism in no case goes further than the circumstances of the parasitic life require. Step by step we can see how, under such circumstances, animals that feed usually on organic detritus, like the Asellidæ, or lead a predatory life like the free-living Copepoda (represented in our waters by the genus *Cyclops*),[2] exchange their free life for a parasitic one. Often they are only temporary parasites, differing from the most nearly related forms perhaps only in the possession of more powerful hooks, whilst in other cases they continue for a longer period upon their host. They lose the power of locomotion they previously possessed, since their extremities atrophy in consequence of disuse, and become stunted in their growth

[1] I have followed in the account given above the usually accepted view, but I may add that the transformation of the snail into the so-called snail-sack, has not as yet been directly observed.

[2] See v. Nordmann, *Mikrographische Beiträge*, Bd. ii. : Berlin, 1832.

according to the degree to which their parasitism becomes stationary. Likewise, also, the sensory perceptions, with their corresponding organs, degenerate. The body loses its segmentation, and finally becomes changed into a cylindrical mass, which not only swells considerably under the pressure of the rapidly growing sexual organs, especially the ovaria, but often becomes deformed in a most irregular manner. Such extreme cases are exhibited among the Copepoda by the Lernæadæ,[1] among the Isopoda by the Entoniscidæ,[2] which live an entirely entozootic life.

But even in these extreme cases the parasitic Crustacea possess, in their young state, the same organization as do the allied free-living forms, and, with a similar form, they lead also at first a similar life. The transformation into the definitive condition is slow and gradual, and is brought about by a metamorphosis which runs parallel with every change in the relations of life.[3] That the metamorphosis is retrogressive on the whole, and that it advances to different degrees according to circumstances, has been mentioned above; I will only add that—in correlation with a previously mentioned fact (p. 44)—it often reaches a higher degree in the female than in the male.

In the same manner also, as in the case of the parasitic Crustacea, the natural relations of the Gregarines, of the itch-mites, and of the mosquitoes, may be determined to the free-living forms related severally to each of them. But among the parasitic insects there are forms in which the relations are less evident, and the intermediate connecting links are wanting. For instance, the lice and fleas stand, notwithstanding their large number of species, to a large extent isolated from their related forms. They possess characteristics so different that no connecting links have as yet been found, so that even the systematic position of these animals appears in no way determined. The same is the case with the greater number of the so-called intestinal worms. The groups Cestodes, Trematodes, and Acanthocephala consist entirely of parasites, although they differ from each other in the degree of their parasitism, especially the Trematodes. The tape-worms and Acanthocephala are capable only of a parasitic life, through the want of a mouth and alimentary canal; for a free life presupposes the capacity of taking up nutritive substances into the body directly by means of a permanent or temporary opening.

Among the intestinal worms there is only a single group which

[1] C. Claus, "Beobachtungen über Lernæocera, &c.:" Marburg, 1866.

[2] Fr. Müller, *Archiv für Naturgesch.*, Jahrg. xxviii., Bd. i., p. 10, 1862; *Jenaische Zeitschr.*, Bd. vi., p. 53, 1867; and Buchholz, *Zeitschr. f. wiss. Zool.*, Bd. xvi., p. 103, 1866.

[3] See Claus, "Beiträge zur Kenntniss der Schmarotzerkrebse," *Zeitschr. f. wiss. Zool.*, Bd. xvi., p. 365, 1864.

has related forms living in the free state, and that in considerable numbers, namely, the round-worms, or Nematodes. But the free-living Nematodes have only recently become the subject of a close investigation.[1] Only a few decades ago, scarcely half a dozen of these forms were known, and these only imperfectly, so that naturalists, mistaking their natural relations, were inclined to class them with the Infusoria rather than with the Nematodes. Under such circumstances it seems easy to understand how the older helminthologists entertained the view that the internal parasites stood isolated, not only biologically but also systematically, from other animals. They united them into a single class (Entozoa), which, although nearly approaching the free-living worms, was understood to have no close relation to them. It will be obvious that such a connection helped greatly to displace the processes of entozootic life from their natural connections. Under its influence parasitism appeared in science as a phenomenon *sui generis*, which could not be judged according to the laws of ordinary animal life, but, on the contrary, was thought to be opposed to these in many of its relations. On a former occasion (p. 22 *et seq.*) it has been shown at length how for a long time special and peculiar laws were supposed to govern the existence and origin of the Entozoa, and howthese had been invented, for the most part by systematic helminthologists, until they ultimately learned to judge facts more correctly and more in accordance with nature; and thus the relations of the Entozoa to the free-living animals have found a more proper recognition.

As has been mentioned, the relations are most evident among the Nematodes, which are a group of animals whose representatives, far from being exclusively Entozoa, have in the free state such a wide distribution, and under such varying circumstances, that the number of parasitic forms, although also great, is far outbalanced by the former. It would, of course, be impossible here to attempt a full description of these free Nematodes. For our purpose, it will be sufficient to remark that they live in the sea, in fresh water, in mud, and in the earth; and that sometimes they lead a predatory existence, at other times they live on decaying matters. To the latter belong the best known and most widely distributed forms, the species of Dujardin's genus *Rhabditis*, above mentioned (*Leptodera; Pelodera*, Schneider). They are animals of small size, which live everywhere in large numbers where the earth is impregnated with decaying organic substances, and differ from their related forms, especially in the structure of their alimentary and sexual organs. Especially characteristic is the highly muscular œsophageal tube, which encloses in its posterior

[1] Especially by Bastian, Ebert, Schneider, Bütschli, Marion, and de Maan.

globularly expanded portion (the so-called "Bulbus") an armature usually formed of three valvular teeth (Fig. 60). Sexual maturity is attained only through abundant nutrition, mostly only in places where a mass of decaying matter has been formed. In such localities the generations follow upon one another often so closely, that the young worms may be found there in large numbers and in all stages of development. When this decaying matter ceases to exist, either through being exhausted or dried up, then the creatures scatter and continue in the larval state, until some favouring fortune grants them the possibility of further development. In this young state, provided with a cystic larval membrane (with occluded mouth and anus), they can withstand desiccation for a considerable time without perishing. Under certain circumstances these mouthless larvæ reach the interior of living animals, where they then, evidently in consequence of their parasitism, enter upon a course of development which differs considerably from their usual life-history. This is specially the case with a species which was first described by its discoverer, Schneider, under the name *Alloionema appendiculatum*,[1] though he has more recently correctly recognised it as a *Rhabditis* (*Leptodera*).[2] The researches of Schneider, and more especially of Claus,[3] show that the parasitism of this interesting form is a purely optional one, and that it can be abandoned without change of its specific characters. In the latter case the life-history follows the ordinary course; but it is otherwise when the larvæ have the opportunity of migrating into the black slug (*Arion ater*). In this they develop into animals which reach double their size (over 4 mm.), notwithstanding the absence of a mouth; they also lose the chitinous œsophageal teeth and awl-shaped caudal point they formerly possessed, but there develop instead two finely streaked long cuticular bands at the posterior extremity of the body, whose function is most probably that of organs of touch, seeing that they occur also in other Nematode larvæ in this position.[4] The parasites, however, attain

Fig. 60.—*Rhabditis terricola*. Adult female and young.

[1] *Zeitschr. f. wiss. Zool.*, Bd. x., p. 176, 1860.

[2] "Monographie der Nematoden," p. 159 : Berlin, 1866.

[3] "Beobachtungen über die Organization and Fortpflanzung von Leptodera appendiculata :" Marburg u. Leipzig, 1868.

[4] See Vol. II.

sexual maturity only after abandoning this host, when they cast their skin, and lose their riband-shaped caudal appendages, while the apertures of the alimentary and sexual organs break outwards through the cuticle. In the sexually mature state also the size and formation of the tail characterise these animals as a peculiar form. Even the internal organization shows many differences. The uterus contains at least 500 to 600 eggs, whilst in the female developed from the free larva it encloses two or three dozen eggs at the utmost. In both cases, however, the eggs develop within the body of the female into embryos, which are exactly alike in size, form, and organization; and may also attain to sexual maturity in the free state in the presence of nitrogenous food material, without the need of migration into slugs. Hence there is no doubt that the parasitism in this case is merely collateral with the free state, and is of importance in the maintenance of the species only so far as—in agreement with the relations previously indicated—it affords the possibility of producing a more numerous progeny. At the same time it is evident that the deviations in the structure of the parasitic generation are in correspondence with the altered circumstances of its life, and are conditioned by them.

The appearance of parasitic generations side by side with free-living ones, which in the case of the above-mentioned *Rhabditis appendiculata* was only possible under certain circumstances, is more conspicuous in other instances, and becomes ultimately a constant phenomenon. The parasitic generations intercalate themselves between the free-living, in regularly alternating succession, just as do the so-called "nurses" between the sexual animals in the case of alternation of generations. But the intermediate generations are not asexual like the nurses, which, as is well known, produce their successors asexually, but they are complete sexual animals, equivalent morphologically to the free-living generations, and in some respects even occupying a position superior to them.[1]

Such is the case with the above-mentioned *Rhabdonema* (*Ascaris*) *nigrovenosum* (p. 2), whose *Rhabditis*-form, living in the excrement of frogs, differs very little from the animals related to it. Like other species of *Rhabditis* of small size (Fig. 61), it attains sexual maturity within a short time, and produces several embryos, which are hatched within the body of the female, and, as has also been observed in the case of other Rhabditidæ, remain there until they have completely destroyed and devoured the internal organs. Also, at the com-

[1] I have for some time been accustomed to call such an alternate succession of dimorphous sexual generations by the name "Heterogeny."

mencement, the young have the characteristics of the genus *Rhabditis*, but lose them while yet in the maternal body; after they have attained a certain size, they cease to eat, and undergo further development only after having found an opportunity of becoming transferred into the lung of a frog, and thus exchanging their former mode of life for a parasitic one.

The adaptation to the circumstances of parasitic life is much more complete in these worms than is the case in *Rhabditis appendicu-*

FIG. 61.—Rhabditoid form of *Rhabdonema* (*Ascaris*) *nigrovenosum*. *A*. Male ; *B*. Female, with embryos in various stages of development.


FIG. 62.—Mature embryo of *Rhabdonema nigrovenosum*.

lata. When they reach the lungs of their host, the young parasites grow to a length of almost an inch, and possess scarcely the slightest

trace of similarity to their predecessors; they live for several months, during which time they produce a countless number of eggs, which are hatched while yet in the uterus, and afterwards pass into the intestine of their host. During their stay in the intestine the embryos escape from the shell; they again become small perfect Rhabditidæ (Fig. 62), and remain in this form in the cloaca, unaltered, until they are expelled with the excrement, when, if surrounded by putrescent matters, they complete their life-cycle in a few days. The remarkable circumstance that the parasitic *Rhabdonema nigrovenosum* is always found only in the female form, at first led me to suppose that they propagate their species by parthenogenesis; but I have since found—as also Bischoff had previously done—that in several individuals there were seminal corpuscles in the posterior portion of the ovary among the eggs; so that I am now prepared, with Schneider and Claus, to regard this form as a hermaphrodite, which, as is also known to be the case in certain instances of free-living Rhabditidæ,[1] produces seminal corpuscles in sexual organs of otherwise female structure for some time before the ova make their appearance. But I must add, that in many cases I have sought in vain for these seminal corpuscles; and other helminthologists have also experienced the same difficulty—*e.g.*, von Siebold—so that the sibility of a parthenogenetic development is not yet entirely excluded.

[It was to be expected *a priori* that *Rhabdonema nigrovenosum* could not be the only Nematode possessing so peculiar a life-history; but the statement of Ercolani[2] as to the descent of the *A. inflexa* and *A. vesicularis* of hens from certain free-living *Rhabditis*-forms, has no foundation in fact. On the contrary, my recent researches[3] lead to the conclusion that the so-called *Anguillula stercoralis* (an unmistakeable *Rhabditis* found in the excreta of patients suffering from diarrhœa in warm countries, and especially Cochin-China) produces sexually a new generation, which becomes transformed in the intestine into the so-called *A. intestinalis*, represented, like *Rhabdonema nigrovenosum*, only by female individuals. The same is true of a sausage-shaped anenteric Nematode (*Allantonema mirabile*, Leuckart[4]), which is parasitic in the body-cavity of *Hylobius pini*, and con-

[1] See Schneider, "Monogr. d. Nematoden," p. 313; and Vernet, *Arch. Sci. Phys. Nat.*, t. xlv., p. 61, 1872.

[2] Ercolani, "Sulla dimorphobiosi, &c.," *Mem. Accad. Bologna*, t. iv., p. 237, 1874, and t. v., p. 391, 1875; Abstr. *Journ. de Zool.*, t. iii., p. 67, t. iv., p. 254.

[3] Leuckart, "Ueber d. Lebensgesch. d. sog. Anguillula stercoralis, u. deren Bezieh. zu d. sog. A. intestinalis," *Bericht d. math. phys. Cl. k. Sächs. Gesellsch. Wiss.*, pp. 75-107, 1882.

[4] Leuckart, "Ueber einen neuen heterogenen Nematoden," *Bericht d. Versamml. deutsch. Naturf. Magdeburg*, p. 320, 1884; a more detailed account will shortly appear in *Bericht. d. math. phys. Cl. k. Sächs. Gesellsch. d. Wiss.*

tains in the uterus-like terminal portion of its generative organs an innumerable quantity of Rhabditoid embryos, which become free by boring to the exterior, and grow into mature males and females without essential change of form.—R. L.[1]]

But even the single example of *Rhabdonema* is sufficient not only to place beyond doubt the special relations between parasitic and free life, but to prove further that the former, instead of being collateral, or even subsidiary to the latter, as in the case of *Rhabditis appendiculata*, may, under certain circumstances, become more conspicuous; the importance of the free life, of course, becoming less in the same proportion.

This alteration in the relative importance of the two conditions of life has by no means reached its extreme point in *Rhabdonema*, for, according to the above-mentioned (p. 61) researches, there is a whole series of parasitic Nematodes (especially in the family Strongylidæ), among which the *Rhabditis*-form, instead of representing an indepen-

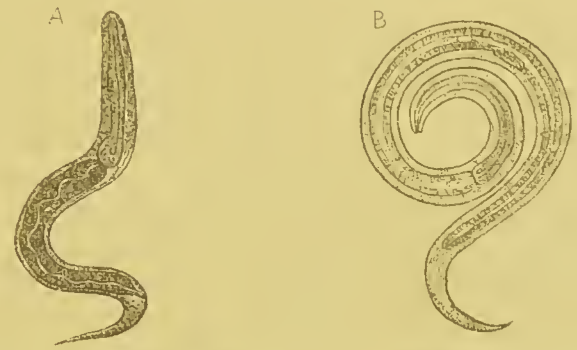


FIG. 63.—*Dochmius trigonocephalus*. *A*. Free-living young form ; *B*. Young parasite.

dent generation which precedes the parasitic, is limited to the young stage of this latter, and passes on at once into the parasitic condition. After the manner of the common Rhabditidæ, these worms live at first free in mud and damp earth, where they feed and grow until they have attained a definite size. With the shedding of their skin the characters of the genus *Rhabditis* are lost, and also the possibility of their former mode of sustaining life. The worms, however, continue to live for some time under the former conditions, but only so long as the reserve material gathered in their interior is sufficient to meet their necessities. In order to grow further, and to complete their metamorphosis, they must exchange their former free life for a parasitic one, and only in the interior of a living animal do they find the conditions for their complete development.

[1] The above passage has been substituted by the author for one in the German edition. —W. E. H.

Notwithstanding all differences, the constitution of the young form points unquestionably in all these cases to the relations which obtain between it and the Rhabditidæ. The differences, moreover, are not so great as they might seem at first sight, for, on the whole, they are limited to the fact that the former condition of life, which was spread over two generations, is now drawn together into one; and this is a phenomenon which we often meet with in animal life. I need only remind the reader, by way of example, that in nearly related forms the alternation of generations is often represented by a metamorphosis in which the former preliminary generation is represented only by the characters of the young form.

But even these traces of a former independence may be more or less completely lost, for we know that besides the species with alternation of generations and metamorphosis, there are very often others in which the state which was passed through by the former as a free larva is relegated to the period spent *in ovo;* so that thus birth occurs at a stage of development which was previously attained only in the free state. In such cases, of course, all those properties remain latent which enabled the respective conditions to obtain external manifestation; and the form which in the previous case was living and mature, is now indicated only in such faint outline as is necessary for accomplishing the transit into a new stage of development. Such being the case, we have, then, no right to make the existence of a *Rhabditis*-like larva the exclusive criterion for the relations which obtain between the parasitic and free-living Nematodes. By means of a continuous and ever-increasing adaptation to the conditions of parasitism, this larval form may disappear, or, more correctly, it may become unrecognisable in the processes of development *in ovo.* Through such abbreviations of the history of development there may then arise forms like *Oxyuris*, *Trichocephalus*, *Spiroptera*, and others, with embryos, which are not hatched in a free state, but remain in the egg until they have found a host (p. 66).

The differences which exist between these species must of course be considered in exactly the same way as the specific differences between free-living creatures. In every case the characters of an animal are the factors which determine its mode of life; so that if two animals deviate from each other, their capacities also vary, and that in exact proportion to the degree in which they differ *Trichocephalus* and *Spiroptera* live under other conditions than *Oxyuris.* Although they are all Entozoa, and even inhabit the same organs, yet they differ in manner of locomotion, nutrition, and propagation, as well as in other functions. It is these very differences which find expression in the peculiarities of the external and internal structure, since the

animal-body is plastic, and capable of adapting itself to the conditions of a specific mode of life. Hence we must leave it doubtful whether the unmistakeable similarity which *Oxyuris* (Fig. 64) presents in many respects (especially in the form of the body, structure of the alimentary canal, and sexual apparatus) to *Rhabditis*, is the consequence of such a secondary adaptation; or whether it may be interpreted as a mark of closer genetic relation. But it is not only the developed animals which present such conditions of adaptation, but also the embryos. Whether these remain where they have become free, or forsake the place of their birth and migrate; whether in their migration they break through tissues and organs of a particular character; whether their locomotion be rapid and energetic or not;—all this finds expression in form and structure, and often expresses itself in forms which, notwithstanding a common type, frequently differ widely from each other.

FIG. 64.—*Oxyuris ambigua* (young).

In this way may also be explained the fact that there are Nematodes whose embryos exist without a *Rhabditis*-form for a time in the free state, until they migrate into their host in some way or other. Such embryos do not lead a true free life, like the Rhabditidæ, for they neither feed nor grow, but resemble free-living animals, in so far as they have the power of independent locomotion. It is owing to this circumstance that they are able to escape many of those casualties which otherwise determine the distribution and transference of helminthic germs. There are, then, certain advantages connected with such a larval form, and it may be these which have brought about its existence. It is plain that the form and structure of the embryos change in manifold ways, according to the varying conditions (locality, mode of locomotion, character of the skin to be penetrated); and this fact is obvious on even a superficial examination of the embryonic forms, say of *Cucullanus* or *Dracunculus* on the one hand, and *Strongylus filaria* on the other (Fig. 65), and may be established even by a most superficial research. The impossibility of obtaining nutriment naturally makes it necesssary in all cases that the duration of such larval stage must be short; and, generally, the shorter the more lively is the locomotion which the embryo exhibits.

I must of course leave it undetermined whether I have succeeded in the above attempt to develop the phenomena of the parasitic life among the Nematodes in correct and natural sequence,

from their earliest manifestation. Owing to the impossibility of checking reasoning by experiment, all such attempts have a more

FIG. 65.—Embryos, *A.* of *Cucullanus*, and *B.* of *Strongylus filaria.*

or less subjective character. It was not my intention to draw up a phylogenetic tree for the parasitic Nematodes, since that could be done only in reference to their relations, and might prove illusory in a very short time. What I aimed at was not more than to prove the possibility of such a relationship between the free-living and parasitic Nematodes as would clearly allow of a derivation of the latter from the former, on the basis of biological knowledge.[1] I will therefore also grant that the connections may with equal, and perhaps even greater, right be sought in other directions than that followed by me. Thus, for instance, one might perhaps interpret the freely moving larvæ which I mentioned last as being allied to the *Rhabditis*-like condition of other Nematodes, instead of explaining them to be only a subsequent adaptation, as I endeavoured to do; and one might, by the hypothesis of one diminished function (merely of locomotion), derive them from other Nematodes, and thus regard them in a certain way as degenerated *Rhabditis*-forms. But in fact this is somewhat deceptive, especially when one considers larval forms of certain species of Strongylidæ, which, both by their organization and the systematic position of their parents, remind us strongly of the *Rhabditis*-like embryos of *Dochmius* and other Nematodes. Still, as above mentioned, these are only possibilities, and hence remain always arbitrary. But thus much is established, that the parasitism of the Nematodes

[1] Bütschli has attempted in a similar way to prove the relations that exist between the free-living and parasitic Nematodes.—*Bericht d. Senkenb. naturf. Gesellsch.*, p. 56, 1872.

exists in various degrees, and, as a rule, attains its complete development only at the expense of a free life.

The most complete case of this parasitism has not, however, hitherto found a place in our exposition. I refer to *Trichina*, which, as a rule, completes its entire life-history in the body of its host. The embryos, which are born alive, soon bore through the wall

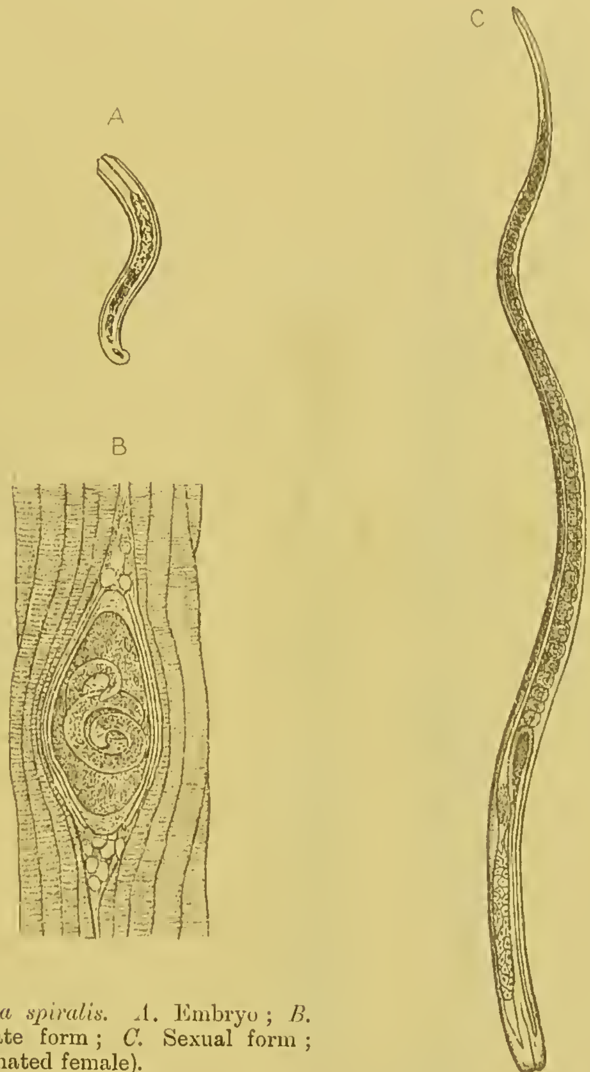


FIG. 66.—*Trichina spiralis*. *A*. Embryo; *B*. Intermediate form; *C*. Sexual form; (unimpregnated female).

of the intestine which shelters their parents, and thus reach the muscles, where they develop into a larval form, which, after transference into another suitable host, directly completes its growth into the sexual form (Fig. 66). A lengthened existence in the free state is thus entirely excluded; even embryonic development and migration occur during the period of parasitic life. It is exceptional, and only

in rare cases, that embryos expelled from the body along with the fæces can effect a transference.

The *Trichinæ*, indeed, furnish the only instance of a parasitism which has lost every relation to the outer world. The Trematodes and Cestodes, as well as the Acanthocephala, are, without exception, governed by the law that in their young conditions

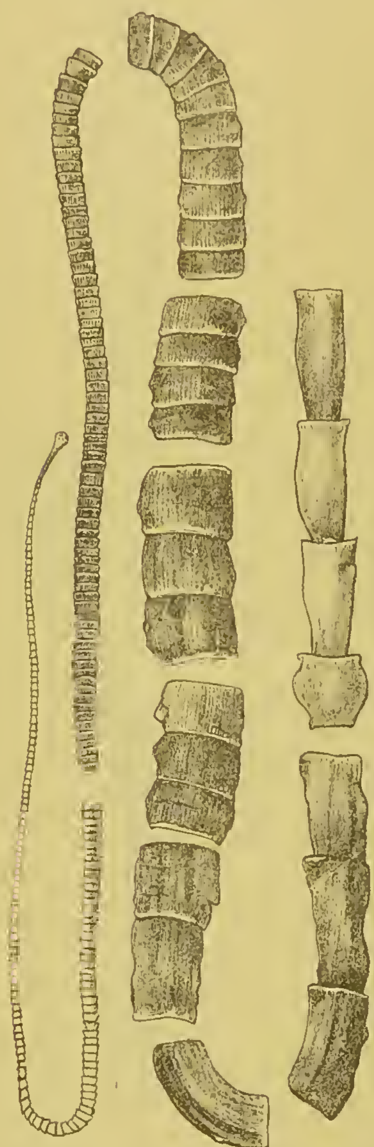


FIG. 67.—*Tænia mediocanellata* (natural size).

FIG. 68.—*Distomum hepaticum* (natural size).

they reach the external world either as freely-moving embryos, or at least as eggs, and from thence they return into their hosts, by means either of an active or passive migration. We know of no case,

however, in which, among these Helminths, the free life of the larva attains to greater biological independence than I have proved in various ways to be the case among the Nematodes. Where we do meet with a free larval form among them, its function is limited to the search for and invasion of a suitable host (p. 61). Everywhere, during this period of free life, nutrition and growth are in abeyance.

It is evident, and has indeed been mentioned above, that on account of this fact the proof of the relations to free-living animal forms is made considerably more difficult. On account of an extensive adaptation to the conditions of parasitic life, the systematic characters of the animals in question are considerably modified, and often rendered wholly unrecognisable.

Among the groups here mentioned there are two, the Cestodes and Trematodes, which are very nearly related to each other, so nearly indeed, that it is difficult to draw a clear distinction between them. This announcement may seem startling, when merely the external form of a *Tænia* (Fig. 67) and of a *Distomum* (Fig. 68) is taken into consideration, for at first sight there are scarcely two other Helminths which differ so widely from each other in their external appearance.

In one case, we find a ribbon-like body, perhaps some metres in length, with head and segments; in the other, a body short, simple, and flat; in the one, suckers on the circumference of the head, in the other, in the middle line of the anterior portion of the body; in the former, an absence of mouth and of intestine, in the latter, a well developed alimentary apparatus. Who, at first sight, would expect to find resemblances among such opposing characters? But the question assumes another aspect, when we recognise that what we call a tape-worm is not a single animal like a caterpillar or millipede, but a whole colony, which furnishes segments in regular succession, immediately behind the so-called "head," which also represents a specialised individual—the "Scolex" (p. 37). Not the whole worm, but the single segment (Proglottis) must be compared with the fluke; and then we shall find, especially in the structure of the sexual apparatus, which constitutes by far the greatest portion of the whole internal organs, that there are so many and such surprising similarities, that the close relationship can no longer remain doubtful. Of course there are certain differences between the two forms, especially in respect of the intestine and of the organs of attachment, but even these lose their importance as soon as we extend our comparison over a large number of species.

In the first place, it has been shown that among the entoparasitic Trematodes there are a number of species which, like the

Cestodes, have no alimentary canal.[1] In the case of a large free-living animal such a want would, of course, be a very remarkable circumstance, since the possession of mouth and intestine is, according to our present knowledge, a most necessary requisite of such animals. But the relations of parasitic life, which permit of nutriment being taken up through the skin, render the possession of these organs unnecessary, or at least not indispensable (p. 18). Even in Nematodes we see the intestinal canal become atrophied in a few cases. This proves no more than that the parasites in question are so completely adapted to the conditions of their existence, that they have no further need for an intestine, and hence we can only interpret the absence of this organ in the Cestodes as meaning that they are much further removed from the conditions of free life than the Trematodes.

But the absence of hooks in the proglottides, like the absence of an intestine, results from the relations given above. They do not stand in such need of them as the solitary living Trematodes, since they belong to a community which is sufficiently firmly fastened by means of a hook apparatus, with which the so-called head is provided (Fig. 4); the individual segments of the chain have thus a certain share in the hook apparatus situated on the head.

If further proof of this assertion were required, it might be found in the existence of certain unsegmented Cestodes, which, like *Caryophyllæus, Amphiptyches*, &c., represent in their simple body both head and proglottis,—that is, unite in themselves both a hook-apparatus and sexual organs like the Trematodes. That which in the common tape-worm was spread over two generations (head and sexual animal) has in these animals again become united in a single individual: and this has been pointed out above to be a frequent occurrence among these groups which present alternation of generations—for it is an alternation of generations which manifests itself in the mode of development of the tape-worms.

The above-mentioned facts leave no room for doubt that the Cestodes are very closely related to the Trematodes, that they represent in a certain sense Trematodes without an intestine, in which the organism has, according to the law of alternation of generations, separated itself into two genetically combined individual forms. That this affords certain advantages of great importance, especially to animals exposed to so many vicissitudes, as is the case with the intestinal worms, is apparent, especially when we remember that the young tape-worm (Scolex) is rendered capable, through the alternation of

[1] Such is the case, according to a letter which I have received from Prof. Claus, in a Trematode allied to *Distomum* from the intestine of *Delphinus delphis*, as also, according to van Beneden, in *Distomum fillicolle*. Dr. Taschenberg will shortly prove that these examples by no means complete the list of anenteric Trematodes.

generations which it undergoes after transference to its definitive host, of multiplying the number of its descendants by the number of the sexual animals which it produces. This fact also proves that the tape-worms are Helminths, which have adapted themselves much more completely to the conditions of parasitism than the Trematodes.

If tape-worms are in reality to be regarded as creatures which have sprung through a further adaptation to the conditions of parasitic existence, from Trematodes or Trematode-like ancestors, then the question regarding the origin of these two groups resolves itself into one—that is to say, the inquiry concerns itself only with the relations which the Trematodes bear to free-living worms.

In the discussions of this question only two groups of known animals can be considered here; these are the leeches and the Planarians, both of which show in their external appearance and internal structure a manifold resemblance to the Trematodes. The leeches, by their mode of life, show an analogy with the Trematodes, for it is well known that the greater number of them live as parasites, although they are to some extent predatory (*Aulastomum vorax*, for instance, feeds chiefly on earth-worms and snails). The smaller and weaker forms of leeches are almost as persistent in their parasitism as the ectoparasitic Trematodes, some of which they also resemble in size and appearance (*e.g.*, *Astacobdella*, which is parasitic upon the cray-fish, and *Udonella* parasitic upon *Caligus*). One might indeed be easily tempted to imagine a direct connection between these two groups.

But upon closer comparison there are considerable difficulties opposed to this hypothesis. Not only do the leeches possess a distinctly segmented body—the segmentation being evident also in their internal structure, especially in the formation of their nervous system and excretory organs—but also the mode of their development and the organization of their embryos manifest many and vital differences from the Trematodes, which at present forbid any attempt to connect them. What similarity there is between the two forms is either more apparent than real (structure of the intestine and sexual organs), or is only found in points of inferior importance (possession of suctorial discs, absence of body-cavity). It is evidently more in accordance with our present knowledge of the morphological relations of the Hirudinea to regard them as parasitic forms allied to the earth-worms, than to connect them with the Trematodes.

But if the Hirudinea do not furnish a link to the Trematodes, there remain only the Planarians which can be regarded as their ancestors. These prove in reality to be very closely related to the Trematodes in their general structure, and the formation of their individual organs. In both cases, the short unsegmented parenchyma-

tous body contains a many-branched alimentary canal without anus, and with a powerful pharynx and a strongly developed hermaphrodite sexual apparatus. The same agreement obtains in the structure and arrangement of the excretory vessels, the nervous system, and the muscles. Even in respect of the histology there are many similar agreements. Finally, since the embryonic conditions also manifest great similarity to each other, there remains a difference between the two groups, only inasmuch as the one consists of free-living animals, the other contains only parasites. The specific peculiarities, however, of the Planarians, as well as of the Trematodes may be ascribed to this difference; since the possession of a ciliated epithelium and special organs of sense, as we find them in the Planarians, correspond with the requirements of a free life, exactly in the same way as the presence of a hook-apparatus does to the conditions of parasitism. The free swimming young forms of the Trematodes—even their entozootic species—are mostly provided with the ciliated epithelium of the Planarians, and often also with the eye-specks of their free-living relatives (Fig. 69).

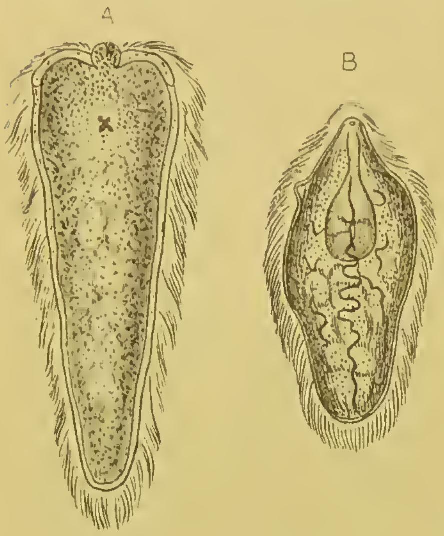


FIG. 69.—Ciliated Embryos of *A*, *Distomum hepaticum*, and *B*, of *Monostomum capitellatum*; the former with an eye-speck.

There are forms, even in the fully developed condition, which serve as connecting links between the two groups. As there are numerous species of Trematodes which, instead of inhabiting the internal organs, live upon the external surface of their host, and approach free-living animals in their pigmentation and possession of eyes, so also we are acquainted with Planarians, the posterior extremity of whose body presents a discoid organ of attachment (*Monocelis caudatus*, Oulian.), or even bears a true sucker (*Monocelis protractilis*, Greeff), by the help of which they attach themselves to foreign bodies. Leidy erects the Planaridæ, with a suctorial disc at the posterior extremity of the body, into a distinct genus (*Bdellura*), and describes in it a species (*Bdellura parasitica*) which lives on the gills of *Polyphemus occidentalis*, and presents an instance of a true parasite.[1] Apart from the ciliated epithelium, it

[1] Here may also be mentioned *Malacobdella*, which was for a long time classed among the Trematodes, and, like the Entozoa, is parasitic in shell-fish, but notwithstanding belongs

would be difficult to distinguish such forms from ectoparasitic Trematodes. But this ciliated coating is lost as soon as the parasitism becomes stationary or permanent, and the change of the host takes place only during the larval period.

After these observations, the relationship of the Trematodes to the free-living Planarians may be taken as established, so that I may omit a comparison of the young forms of these two groups. I will only mention that the above described (p. 30) peculiar developmental relations of the embryos of *Monostomum mutabile* occur also in certain worms[1] closely related to the Planarians, perhaps even in the Planarians themselves. Likewise the fact that the embryos of the entozootic Trematodes often leave the egg without a differentiated intestine, and sometimes (namely, when they develop into the so-called "sporocysts," Fig. 49, p. 71) never possess such an organ, will hardly seem peculiar in creatures resembling the Planarians. It has been proved that there are forms among the free-living Planarians which are devoid of a proper intestine (Acœla, Oulian.), its place being occupied by a readily moveable mass of protoplasm, which absorbs the nutriment that passes in through the mouth, as is well known to be the case in the Infusoria.

The absence of an intestine in the internal parasites is thus not in all cases the result of a retrograde development, but, under certain circumstances, also the sign of an imperfect differentiation; and this is the case not only in the embryos of the above-mentioned Distomidæ, but also in those of the tape-worms, in which it is impossible to find even the rudiment of an intestine.[2] This is a further proof that these latter animals are far more completely adapted to a parasitic life than the other related parasites. This is much more strikingly shown in the Tæniadæ, however, than the Bothriocephalidæ, by the fact that the former do not even possess the embryonic ciliated coating which is seen in the young forms of the latter (Fig. 70), as in the Trematodes,[3] and which, as in these, subserves the function of free locomotion. The

(as had been supposed to be the case by me in 1848) to the Nemertines, a group closely related to the Planaridæ.

[1] In this connection, see the observations concerning the so-called "Desor's Larva," Max Schultze, *Zeitschr. f. wiss. Zool.*, Bd. iv., p. 179, 1853; and Krohn, *Müller's Archiv f. Anat. u. Physiol.*, p. 293, 1858, and especially Barrois, "Mém. sur l'embryologie des Némertes," *Ann. Sci. nat.*, sér. 6, t. vi., p. 1, 1877.

[2] Huxley considers this circumstance so important, that it causes him to doubt the origin of the Helminths without intestine from animals with intestine; and he throws out the suggestion that they may be independent of free forms, and be directly and continuously developed forms, that were from the commencement parasites without intestine. See "Anatomy of Invertebrated Animals," pp. 213, 652, 675: London, 1877.

[3] In many cases also among the Trematodes, and even Distomidæ, the embryos are without a ciliated coat. Von Willemoes Suhm classes among the 28 known embryos of Trematodes 10 non-ciliated forms (*Zeitschr. f. wiss. Zool.*, Bd. xxiii., p. 339, 1873).

embryos of the Tæniadæ, like those of the Trichocephalidæ and other Nematodes, reach their hosts while yet enclosed in the egg-shell.

A similar form of parasitism is that of the Acanthocephali, which resemble the tape-worms in having no intestine, and are therefore by many zoologists united with the latter into one systematic group (Anenterati). In favour of such a conception, one might adduce the analogies which obtain between the two groups, and are especially noticeable when the structure and mechanism of the proboscidean hook-apparatus (Fig. 71) of the Tæniadæ, with their cylindrical rostellum, and of the *Tetrarhynchi* are brought into comparison. But all these similarities prove scarcely more than a certain agreement in the conditions of life. They represent merely adaptive relationships, and since the

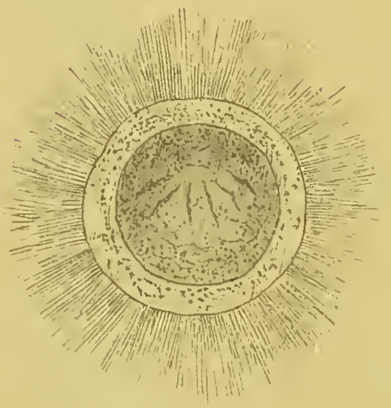


FIG. 70.—Free-swimming embryo of *Bothriocephalus latus.*

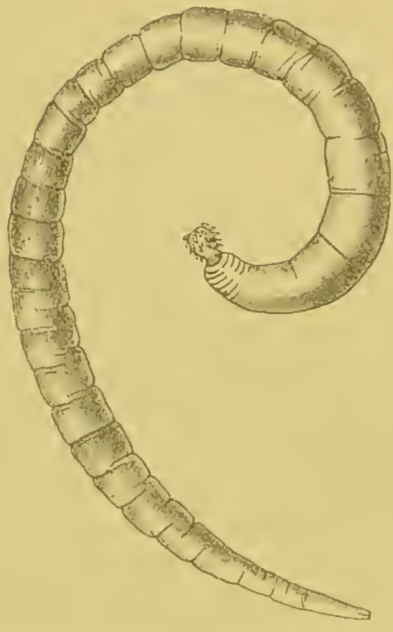


FIG. 71.—*Echinorhynchus spirula*, natural size (after Westrumb).

morphological structure in the two groups manifests the greatest differences, they by no means permit the conclusion of a genetic relationship to be drawn. The presence of a muscular body-wall separated from the internal organs—not to speak of other peculiarities—prohibits their association with the flat-worms.

It is indeed useless to seek in other directions for forms with which the Acanthocephali naturally agree. For a time it was supposed that they were allied to the Sipunculids, and might be regarded as parasitic forms of this group. But in this case also it was only a superficial similarity which gave rise to this view, the more so

as it was confined almost exclusively to the external formation of the body.[1] The internal organization of the Sipunculidæ shows scarcely any close relation to the Acanthocephali, unless the presence of an unsegmented dermal muscular tube be regarded in this sense. Also the fact that the gulf between the two groups is not bridged over by any intermediate forms, further lessens the probability of a relationship between them. We know, however,—thanks to recent researches—of a parasitic animal closely related to the Sipunculidæ, namely, the male of *Bonellia*, which (p. 10) lives as a parasite in the sexual passages of the female; but nothing in the animal betrays approximation to the Acanthocephali. The structure reminds one rather of the condition in the Planarians, or the ciliated embryonic condition of other worms. Also the similarity to the peculiar genus *Echinoderes*[2] is limited to certain external characters (the presence of hooks upon a conical head), and does not justify the opinion of a genetic connection.

But though it must be confessed that no group of animals can be adduced to which the Acanthocephali could be directly traced, this fact does not, of course, in any way involve the conclusion that they have no relation to any other forms. This only may be learned from it, that these relationships, instead of being manifest as in other cases, are of a more hidden nature; in other words, that the Acanthocephali are related to forms of animals which have succumbed to a deep-seated modification before the typical structure of the parasites in question was developed. The dropping out of the intermediate members, of course, causes the position of these worms to appear very isolated. If, from this point of view, we search for forms which might be considered as the starting-point of the Acanthocephali, then our attention will soon be drawn to the Nematodes, which like them are parasitic. I will base nothing on the fact that there are thread-worms which, being provided with a proboscidiform and armed cephalic extremity, have occasionally been considered as *Echinorhynchi*. An erroneous interpretation cannot have the force of proof. But this would have been almost impossible, had not so many other similarities obtained between the two forms. In fact, both possess an elongated cylindrical body, the walls of which are formed of a strongly developed dermal muscular tube, surrounded by a firm integument. This tube is traversed by longitudinal vessels, and encloses a distinct body-

[1] Schneider also attempts to support the relationship with the Sipunculidæ by means of the structure of the muscular apparatus, which in its arrangement differs from the conditions found in the Nematodes, and agrees more with those of the Sipunculidæ (*Müller's Archiv f. Anat. u. Physiol.*, p. 592, 1864).

[2] See especially Greeff, *Archiv f. Naturgesch.*, Jahg. xxxv., Bd. i., p. 72, 1869; and Pagenstecher, *Zeitschr. f. wiss. Zool.*, Bd. xxv., Suppl., p. 117, 1875.

cavity, which in both cases contains a well developed male or female sexual apparatus, whose differences, although apparent even on a superficial view, are scarcely more marked than those found in the structure of the same apparatus in the Chætopoda or the Turbellaria. According to the above remarks, the absence of intestine in the Acanthocephali can scarcely be regarded as an important distinction. But the proboscidiform apparatus also, although of complicated and peculiar structure, cannot form an objection to the existence of a relationship with the Nematodes, since we are acquainted among the Cestodes both with forms provided with and devoid of a proboscis (*e.g.*, *Bothriocephalus*).

In conclusion, we may remember that the Acanthocephali manifest also in respect of their histology many resemblances to the conditions which obtain among the Nematodes. Among other things, both agree in the structure of the muscular fibres and the ganglia, in the cuticular character of the connective tissue, in the often colossal size of their cells, and in the complete absence of ciliated epithelium. On consideration of these facts, it becomes evident that the Acanthocephali must be regarded as peculiarly modified Nematodes. The relations of these two groups may be rightly compared to those which obtain between the tape-worms and Trematodes; that is to say, the Acanthocephali may be regarded as forms of Nematodes which have adapted themselves to the parasitic conditions of existence, to a higher and more complete degree than the others. The character of the young forms agrees with this conception, and we are led to believe that they are more closely related to the original conditions, because they are (according to my observations) provided with the rudiments of an intestine,[1] in which one can discern, notwithstanding its incomplete differentiation, a pharynx and an intestine. An oral aperture is wanting; its place is occupied by a grove in the form of a slit, surrounded by a varying number of setæ, embedded in the retractile cephalic extremity—(Fig. 72). On comparing this young form with the common embryonic forms of the Nematodes, it would seem as though the above asserted similarity were only a slight one; but this opinion changes when we consider the embryos of the genus *Gordius*, in which we meet with relations (see specially the illustrations published by Villot) which in fact differ only very little from those of the embryos of *Echinorhynchus*. *Gordius* is a

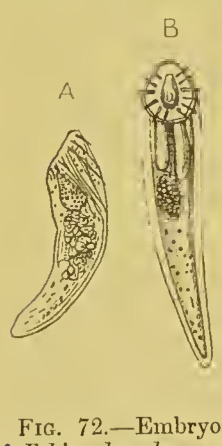


Fig. 72.—Embryos of *Echinorhynchus angustatus*; *A.* the profile; *B.* ventral view.

[1] See Vol. II.

thread-worm which differs from the real and typical Nematodes in many respects, among which may be mentioned the atrophy of the intestine, and the terminal position of the male and female sexual apertures, characters which approximate it to the Acanthocephalidæ. This is, however, only an additional reason for laying greater stress upon it, since we have every reason to consider the Acanthocephalidæ as yet more modified forms.

The changes which lead the embryos of *Gordius* to their ultimate structure are unfortunately yet unknown to us. This fact is the more to be regretted, as they may acquaint us with relations which would bring the strange and in many ways remarkable metamorphosis of the *Echinorhynchi*[1] nearer to the usual process of development than has hitherto been the case. In the meantime, in considering their relationship, we can lay only slight stress upon these peculiarities, for we are well aware that the developmental history often pursues various courses even in closely related animals; in one case it may be direct, and hasten rapidly to its goal, in another, it may reach its conclusion by a circuitous route, passing through metamorphosis and alternation of generations. The course of development of the *Echinorhynchus* is merely a metamorphosis—a metamorphosis, too, than which nothing more thorough and complete could be imagined, since in its course almost everything that the fully developed worm possesses is formed anew out of the older structures.

After the foregoing account, the reader may decide for himself whether, and how far, I have succeeded in discovering the relationships of the Helminths, and in proving that they have originated from free-living worms by adaptation to a parasitic mode of existence. But even suppose the matters just discussed were proved facts, and not mere possibilities, even then much in the life-history of these animals would remain problematical. We could only conclude from this that a worm is capable of exchanging a free life for a parasitic one, and of adapting itself in structure and mode of life to such altered conditions. Instead of a free creature, the worm becomes a parasite, which departs, more or less, from its original form according to circumstances. It now attains sexual maturity in the interior of its host, instead of, as formerly, in the free state. It propagates, and generally, in consequence of the favourable circumstances of nutrition, has usually a very numerous progeny, which pass to the exterior, and perhaps for a time live freely, but finally develop into sexually mature parasites.

This is so in many instances, not only in stationary parasites, but also in many Entozoa, though very seldom; for, as a rule, the first host

[1] See Vol. II.

does not bring the intestinal worm to complete development, but to a certain more or less advanced stage, after which the parasite attains maturity only after transference into its definitive host.[1] The intestinal worms undergo, for the most part, as has been shown at length above, a change of hosts, and in consequence their life-history and development are spread over two or more hosts.

Of this change of hosts we have hitherto taken no account in our discussion, and yet it is clear that it is a process which not only complicates, in an unexpected manner, the phenomena of parasitism, but also requires an interpretation from a genetic standpoint before we can obtain a complete insight into the nature of parasitic life.

At the outset only an ambiguous answer can be given to the question of the significance and mode of origin of the so-called "intermediate hosts," provided that we do not wish to forsake the point of view we have hitherto occupied. The intermediate hosts have either been interpolated subsequently into the life-history of the parasites, or they were originally true definitive carriers, which formerly brought their intestinal worms to sexual maturity, but have since become merely intermediate, because the history of development of the inmates has extended itself over a greater number of stages by means of further formation and differentiation. That we have in both cases to do with a far-reaching adaptation needs scarcely to be expressly mentioned.

If I express myself unconditionally in favour of the second of these possibilities, it is chiefly in consideration of the fact that the fully formed and sexually mature stages of the Entozoa are found, with few exceptions, in the vertebrates—that is, in creatures which have relatively only recently originated. The Invertebrata, of course, are not free from Helminths, but all the hundreds and thousands of species which they shelter are, with few exceptions, young forms, which require transference into a vertebrate in order to complete the cycle of their development. If this do not imply that the intestinal worms have arisen along with the Vertebrata, or that they became extinct in their oldest representatives, with the exception of a few remnants—and both seem unlikely upon unprejudiced consideration—then the only possible conclusion is that the Helminths of the Invertebrata have in course of time changed their character, and have, during their further development in the Vertebrata, become mere larval forms instead of sexually mature animals. In view of these facts, we cannot doubt that the vertebrates afford a much more favourable soil for the development of the Helminths than the invertebrates. We must even admit that numerous forms have originated after the Verte-

[1] See 1 *a* and *b*, 2 *b*, and 3, in the short review at the commencement of this chapter.

brata became separated as a distinct phylum; some, even in relatively recent times, such as the *Trichinæ* and others, whose life-cycle is limited to mammals, most recently of all creatures. In many cases the origin of new Helminths may have gone hand in hand with the transformation, by means of which the hosts have gradually become new species.

That the change of a sexually mature animal into a mere preparatory stage (a larva)—the process which we have adopted to elucidate the change of hosts—is biologically possible, cannot be doubted in view of the analogy of the so-called abbreviated development, frequently mentioned above, and whose counterpart it forms. If a series of different developmental phases may contract into a single continuous process, then, conversely, this latter can also spread itself out into a number of such phases. This is a process to which we must attribute a very important *rôle* in the formation of species; for the present larval forms are to be considered, agreeably with the doctrine of descent, as the original sexually mature ancestors of those species which to-day represent their ultimate condition. The sum of the characters by which these latter differ from the larvæ represents the gain which the original animal has gradually acquired under the changed relations of life, changes which become, as it were, added on to earlier ones, so that the development is protracted, and sexual maturity, which coincides with the conclusion of development, is delayed.

The nature of those Entozoa, which are parasitic in invertebrates in a mature condition, lends a yet more definite support to our supposition. They are, of course, few in number, if we except the entozootic Isopoda and a few others, and confine ourselves to the true Helminths; these belong mostly to the thread-worms. But we may mention also a Trematode living in the fresh-water mussel (*Aspidogaster conchicola*), and a Cestode (*Archigetes Sieboldi*), described recently by me, and found in the body-cavity of *Sænuris*.

All these forms develop, so far as we know their life-history (p. 70), without an intermediate host, and attain their sexual maturity immediately in the first host, as would naturally be the case provided our supposition were correct.

In addition, the development and metamorphosis of these forms are very simple, so that the respective animals are but little removed from their hypothetical original form, and become sexually mature in a condition which in many respects stands on a par with the young and larval forms of their further advanced relatives. Thus the Nematodes, sexually mature, found in invertebrates (mostly omnivorous insects and millipedes), follow closely the Rhabditidæ (*Oxyuris*) in

their development; that is, they resemble forms to which the parasitic Nematodes bear relations, which have led us above to regard them as their forerunners, and which are often seen represented in their young forms. An exception must be made in the case of a single very peculiar species (*Sphærularia*), which lives in the body-

Fig. 73.—*Archigetes Sieboldi.*

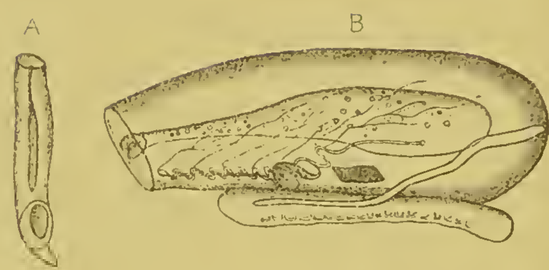


Fig. 74.—*Aspidogaster conchicola.* (*A.*) Embryo, (*B.*) Young animal, not yet sexually mature, (after Aubert).

cavity of the hibernating humble-bee, and shows relations of organization which are as yet only incompletely understood.[1] Likewise

[1] See especially Sir John Lubbock, *Natur. Hist. Rev.*, vol. i., p. 44, 1861, and Schneider, "Monogr. d. Nematoden," p. 322, whose opinions regarding the life-history and morphology of this strange worm differ widely from each other. [Recent investigations of Schneider (*Zool. Beiträge*, Bd. i., p. 1, 1884) have made us acquainted with the interesting fact that the young *Sphærularia* grows outside the body of its host into a sexually mature animal, resembling *Anguillula*, without essential change in its organization. I have convinced myself of the correctness of this observation, and believe I have obtained proof that these worms copulate while in the free condition, and that only the females find their way into the humble-bees, where they develop into the paradoxical *Sphærularia*. If such be the case, *Sphærularia* can no longer be considered an exception to the rule above stated. —R. L.]

Archigetes (Fig. 73) is, morphologically speaking, nothing else than a Cysticercoid—a tape-worm—which concludes its metamorphosis at a stage of development which, in the case of the common Cestodes, represents merely a transitional form inhabiting an intermediate host. *Aspidogaster* also (Fig. 74) is wrongly classed among the otherwise ectoparasitic Polystomidæ, on account of an absence of metamorphosis, whilst its structure stamps it decidedly as a Trematode allied to *Distomum*. *Aspidogaster* resembles a Redia in its mode of development and the formation of its intestinal apparatus in so remarkable a manner, that I see no objection to placing it, notwithstanding its sexual maturity, beside the true Distomidæ, and so classifying it along with them, just as *Archigetes* is placed with the tape-worms. The presence of a ventral sucker can as little be opposed to this conception as the high development of the excretory system of vessels, since both structures must be regarded merely as the result of an adaptation to the animal's mode of life, which cannot be taken into consideration in determining morphological relationships.

The Rediæ and the Sporocysts (Fig. 49), which have sprung from them by a retrograde formation of the intestine,[1] are, in accordance with the above discussion, to be regarded as the oldest Distomidæ, in the same way as the Cysticercoids are the original tape-worms. This agrees with the fact that the Rediæ are more closely related to the ectoparasitic Trematodes (specially by the structure of the intestine) than are the fully formed Distomidæ, and hence may be more easily and readily supposed to be derived from the former. It is, moreover, sufficiently known that the Rediæ do not change directly into the mature Distomidæ, but develop them in their body-cavity out of so-called "germ" cells, which are of the nature of eggs, and separate themselves from the body-wall (Fig. 75). The metamorphosis is divided over two generations, which spring from each other; it thus becomes an alternation of generations, a common phenomenon, as has been shown above. The production of the new brood may perhaps in this case be directly connected with the former

[1] [This supposition has found an unexpected confirmation in the discovery of the Orthonectida (see Giard, *Journ. de l'Anat. et Phys.*, t. xv., p. 449, 1879, and Metschnikoff, *Zeitschr. f. wiss. Zool.*, Bd. xxxv., p. 282, 1881); or rather through the establishment of the fact that these simple animals, parasitic on Ophiuroids and Turbellarians, are to be regarded morphologically as sexually mature Trematode-embryos, devoid of an alimentary canal (Leuckart, *Archiv f. Naturgesch.*, Jahrg. xlviii., p. 96, 1879). Hence the Orthonectida stand at the lowest stage of that series of developmental stages represented by the Trematoda. *Aspidogaster*, therefore, which we have regarded as a sexually mature Redia, stands higher in the series than the Orthonectida. What influence these facts have upon our views of the gradual progress of parasitic life—how beautifully and naturally they come into accord with the views expressed in text—hardly needs any further comment.—R. L.]

existence of sexual generation; in fact, it may in a sense be regarded as the last trace of this process, especially as the germ-cells possess an unmistakeable morphological similarity to ova.[1] The importance which this alternation of generations has for the preservation and distribution of these parasites is evident. Where formerly there was only one parasite there will now originate a number—many dozens, or perhaps even more—all readily capable, under favourable conditions, of commencing new parasitic life.[2]

The newly formed Distomidæ, however, do not grow into sexually mature animals within or beside their parents, but, as a rule at least,

FIG. 75.—Rediæ, with brood of Distomes in the interior. (*A.*) From *Paludina impura* (young and old); (*B.*) From *Lymnæus* (young and old).

forsake the host as a Cercaria, and swim about in the free state for a time by means of an appendage which is not unlike the caudal bladder of *Archigetes,* and then migrate into a new host, generally once more an invertebrate animal (p. 72). The Cercaria thus undergoes a change of host, which does not immediately transfer it to a vertebrate, as is usually the case, but at first to an invertebrate again, such as a snail or a water insect. In the present Distomidæ, also, these two hosts are both

[1] This conception receives a new confirmation from the life-history of *Allantonema,* alluded to above (p. 98).

[2] Such a proliferation in the intermediate host we find in a few Cestodes, and especially in *Echinococcus;* but in this case the young brood originates through budding, and remains connected with its mother-animal in the interior of the body for life.

intermediate hosts, but we may take it for granted that such was not the case from its commencement. On the contrary, these second intermediate hosts brought their Trematodes to sexual maturity in the same way as was formerly the case, according to our supposition, with the Rediæ. Since the caudal appendage, by means of which the Cercariæ swim about, is lost when they force their way into a new host, so the developmental condition of these sexual animals must in the main have been like the present one.

The entozootic Trematodes are accordingly Helminths, in which the change of hosts had already come about at a time when the vertebrates, which are now almost exclusively concerned in it, had not yet come into existence.

The supposition that the Cercariæ originally attained sexual maturity in their hosts, and only later developed retrogressively into more intermediate forms, finds some support in the fact that these animals even now, under certain circumstances, become sexually mature, and produce ova in their intermediate hosts. On a former occasion (p. 73, note) some cases of this kind were cited, and others are continually forthcoming. These sexually mature Helminths are not separate species, possessing no other sexual condition; they are rather nothing more than certain specially privileged individuals belonging to species which, under other conditions, are accustomed to attain their maturity only after transference into a vertebrate.

It is, moreover, a common phenomenon that the Distomidæ not only commence the formation of their sexual organs in the intermediate hosts, but bring them to a state of complete functional capacity. This phenomenon we meet also in other intestinal worms, although individual species present great variations in this respect, so that many are undifferentiated sexually even when passing into their definitive host. With respect to the latter, I may mention *Cucullanus* and *Spiroptera*, whilst others, like *Hedruris* and all the *Echinorhynchi*, assume all their external and internal peculiarities in their intermediate hosts, which is certainly a case of persistence of an earlier state. Of course such differences are not without influence upon the length of time occupied by the development; instead, perhaps, of weeks and months being necessary, as usual, the worm of the latter kind requires only a few days, after leaving its temporary host, in order to attain full maturity, and to acquire the ability to propagate its species by sexual means.

CHAPTER VI.

THE EFFECTS OF PARASITES ON THEIR HOSTS.

Parasitic Diseases.

From what has already been said of the life-history of parasites, and especially of the Entozoa, it is evident that they influence in a most important way the health and even the life of their hosts. But the existence and amount of this influence was firmly established only by the discoveries of recent decades. From this time a rational theory of parasitic diseases, and a true insight into the deep significance of this important branch of medical science, must date. Not that the idea of parasitic diseases was something absolutely new; on the contrary, from the earliest times men knew and feared the injurious effects of these unbidden guests, and feared them perhaps even more than they knew them.

In order to form a correct estimate of the pathological significance of parasites, it is necessary to cast a glance at the literature upon the question of the seventeenth and eighteenth centuries.[1]

There was then no grievous and dangerous malady which parasites, and especially intestinal worms, were not thought capable of exciting. Dysentery, scurvy, hydrophobia, and even the dangerous epidemics of the Middle Ages, such as plague and small-pox, were all described as parasitic diseases. With each disease they associated a particular parasite, just as we now sometimes speak of the cholera-Bacillus, and other similar creatures, as the transmittors of certain specific diseases. They supposed, further, that these originators of disease lived either in the alimentary canal, or under the skin, or in the blood, and thence, according to their nature, infected the whole organism in diverse ways. Nor was this opinion held by individuals only, but by many, and partially even by the most famous representatives of the pathology of the time (Leeuwenhoek, Hartsoeker, Andry, and others).

The possibility of such extravagant opinions is now the subject of incredulous wonder. To understand them it is necessary to realise the condition of medical science at that time. On the one side there was inaccuracy of diagnosis, and almost entire ignorance of pathological

[1] I specially recommend Andry, "Traité sur la génération des vers dans le corps de l'homme," Paris, 1700, of which a new edition and German translation have since appeared.

anatomy; on the other, the natural desire to reduce the different diseases to definite etiological entities. Men then hit upon parasites,[1] as they did later upon magnetism and electricity, in part only because they *knew* so little about them.

It occurred to them the more naturally to refer these diseases to parasites when they observed the exit of intestinal worms and consequent recovery; and also because, since the time of the Arabian physicians, the parasitism of a mite had been recognised as the cause of the widely distributed itch (see Fig. 6). In the eyes of many pathologists, the last-named fact served as direct proof of the correctness of a theory from which they anticipated the weightiest conclusions as to the nature of diseases.

But these hopes were vain. Although helminthological knowledge was gradually more and more extended and consolidated, the idea of the "*Morbi animati*" found no new support. Men attempted in vain to place beyond doubt the existence of a *Contagium vivum* in the above-mentioned diseases. They only formed the conviction that the earlier physicians, with their guesses at the existence of certain parasites, had been much too generous. The so-called "heart-worms" were recognised as blood-clots, the "umbilical worms" as mere fancies. The existence of the itch-mite even was doubtful, since a number of experienced physicians and naturalists had sought after it in vain. Observations concerning the presence of intestinal worms in animals also increased, in which, in spite of this parasitism, no signs of illness were noticed.

Under such circumstances, the earlier opinions became in the latter half of the last century more and more discredited.

The Entozoa were still, it is true, considered on the whole as injurious guests, which might seriously affect the health, and sometimes even endanger the life of their host. But their specific relations to certain diseases gradually ceased to be traced; and there were many who even denied that intestinal worms had any hurtful effects on their host whatever; some even considered their effects to be advantageous. Men like Göze and Abildgaard maintained among other views that intestinal worms aided digestion, by absorbing the mucus and exciting peristaltic contractions. Jördens even called them the good angels and unfailing helpers of children.[2] It was also supposed (*e.g.*, by Gaultier) that their movements and the resulting conditions exerted a favourable influence on the development of the lungs and viscera.

[1] These speculations went so far, that this question, for example, was discussed (and answered mostly in the affirmative)—"An mors naturalis sit substantia verminosa?"

[2] "Entomologie und Helminthologie des menschlichen Körpers:" Hof, 1801.

The belief in the absolute injuriousness of parasites, already shaken by these considerations and doubts, received a still ruder shock, as their wide distribution and frequent occurrence in certain animals became known. Men began not only to deny the existence of specific worm-diseases, but to think themselves justified in maintaining that it was exceptional for the parasitism to cause any disturbance of health. It is true, however, that such opinions were held for the most part by naturalists and helminthologists. The physicians for the most part still held to the old opinions. Wherever there was any doubt as to the nature and origin of a disease, worms were blamed; and "worm-irritation," "worm-fever," and other worm-diseases were very common terms both in theory and practice. And if by chance, or in consequence of medical treatment, a worm left the patient, they considered the diagnosis verified, and the cause of the disease established beyond a doubt.

The professional helminthologists, headed by Rudolphi and Bremser, although, as we have said, decidedly opposing these views, could not deny that certain pathological conditions, especially those of the digestive apparatus, were generally connected with the presence of worms. They were, however, disinclined to believe that these conditions were directly due to worms, but sought, in accordance with their theory of the spontaneous generation of Helminths, to show that there were certain conditions productive of worms. They spoke of a "predisposition to worm production" referable to definite pathological processes, of a "*Diathesis verminosa*," which they sometimes even called "*verminatio*," a worm disease without worms! Thus Bremser,[1] the famous Viennese helminthologist, says, "By a worm disease I mean any disturbance or interruption in the functions of the primary or secondary digestive and nutritive organs, whereby substances are formed and collected in the alimentary canal, which under favourable circumstances may, but do not necessarily, produce worms: I mean, in short, the material factors of worm production. So that worms in the alimentary canal are not an original disease, and indeed can only rarely be regarded as a disease at all, but are much more frequently the sign of the diseased state of the organs in question, or of some interruption in the co-operation of these organs, from which state many results may arise without the presence of worms."

After what has been already said concerning the life-history and origin of the Entozoa, it is unnecessary to criticise these opinions minutely. We may now regard it as completely established that parasites do not originate from a diseased condition, but from germs intruding or introduced, and they especially originate where these

[1] "Lebende Würmer im lebenden Körper," p. 119.

germs find the conditions of their development fulfilled. Just in proportion to the number of germs introduced, and to the adaptation of the environment to their wants, will the number of parasites increase in the individual case.

We might perhaps suppose that the developmental conditions of parasites involved a certain pathological state, and might also assume that parasites could not be developed except in unhealthy organisms; but in the impossibility of all proof this would only be blind adherence to a dogma. It is true that the same has been asserted in regard to the spores of fungi, and even in regard to bark-beetles (*Bostrichus*) and vine-insects (*Phylloxera*), but here also the assumption of a previously existing pathological state seems unwarrantable, having neither proof nor probability.

What leads me most decidedly to this conclusion is the ease with which even the healthiest individuals may be experimentally infected with Entozoa. Of course, the experiment does not succeed with every kind of parasite, but only, as was before explained, with those which find suitable environment. Even then there may be a few cases in which the expected result fails. But our former observations have prepared us for such experiences. For the development of a parasite requires the presence not only of certain specific factors, but also of many individual ones. It might even be granted that the health, and especially the nature of the organism to be infected, are not without effect on the imported brood (in the case above mentioned (p. 85), in which, after three weeks, the heads of *Tænia cœnurus* showed hardly any traces of further change, the animal under investigation had been used some time before for an experiment with *Trichina*), but we have never found the slightest ground for believing that the development of the invading Helminth is promoted or even conditioned by any unhealthiness of the animal experimented upon.[1]

Meanwhile, it is safe to assume that wherever there is a real connection between the unhealthiness of a host and the indwelling parasites, it is the latter who are the efficient causes.

It is, however, not only on *a priori* grounds that we are warranted in maintaining that parasites may cause even very dangerous diseases. Experimental helminthology has securely established this position. I

[1] Statistics, which alone can decide in this case, show, on the contrary, that certain illnesses—*e.g.*, chronic, and especially intestinal catarrhs—tend to remove parasites from the diseased organ, or even to prevent their occurrence. Thus Gribbohm ("Zur Statistik menschl. Entozoen," Kieler Inauguraldissert., p. 8, 1877), in chronic intestinal catarrh, mostly in consequence of phthisical processes, found in 65 bodies only 16 (24·6 per cent.), and in chronic catarrh of the large intestine in 18 bodies only 3 (16·7 per cent.) cases of the stomachic Nematodes (*Ascaris*, *Oxyuris*, *Trichocephalus*), which are otherwise so very frequently present (on an average in 49·8 per cent. of the cases examined).

refer especially to the experiments made with *Tænia cœnurus*[1] and *Trichina spiralis*, which may well dispel all doubt on the subject. If favourably situated, a brood of these parasites acts like poison, and a large dose is sure to kill the animal.

Through these experiments, not only has a foundation of fact been laid for the study of parasitic diseases, but an exact method of treatment has been attained. While little progress has as yet been made in this direction, we have nevertheless established many new and practically important facts.

In speaking of parasitic diseases, we mean the various disturbances of health occasioned by these creatures, in contradistinction to the views of those who speak as if there were only one "worm-disease"—a specific *helminthiasis*.

Parasites act in very different ways,[2] according to their size and mode of life, as also according to the nature of the inhabited organism. Intestinal parasites produce different symptoms from brain parasites, and the effects of these are different, according as they are situated in the cortical layers of the hemispheres, or in the crura cerebri. In the same way, *Dochmius duodenalis* acts differently from *Oxyuris* or *Trichina*. The effects of many parasites never fail—as, for example, in the case of *Cysticercus* in the eye and *Strongylus* in the kidney; and in the case of others, accidental causes determine whether or not, and in what degree, these effects shall show themselves. Besides the situation of the parasite and the individuality of the host, the number of imported germs in this connection is specially important, and to this, indeed, the effects produced and the dangers incurred are ever proportionate. Thus, it can be easily proved that the frightful symptoms of trichinosis occur only when the parasites live in masses in the alimentary canal, and thence invade the muscles[3] in still

[1] Especially instructive on this subject is the result of a feeding experiment which was made simultaneously in May 1854 by van Beneden in Louvain, Eschricht in Copenhagen, Gurlt in Berlin, and by myself in Giessen, with specimens of *Tænia cœnurus* sent us by Küchenmeister (then in Bautzen). The animals became ill in all the places at exactly the same time, and exhibited exactly the same symptoms. Compare Haubner in *Gurlt's Magazine*, *loc. cit.*, Leuckart, "Blasenbandwürmer," p. 47, or van Beneden, *Comptes rendus*, t. xxxix., p. 46, 1854.

[2] We may take this opportunity of referring to the classical work of Davaine, "Traité des entozoaires et des maladies vermineuses de l'homme et des animaux domestiques"—Paris, 1860, 2d ed. 1877—which contains an almost complete collection of experiments concerning worm-diseases up to date, and is full of interesting particulars. The part of this work treating of natural history is not so good even in the second edition, and contains many errors and anachronisms.

[3] The number of muscle *Trichinæ* in an individual case has been estimated at from 60,000,000 to 100,000,000—a number which, on the supposition that half of the *Trichinæ* are females, and produce on an average 1500 embryos, would correspond to from 100,000 to 120,000 sexually mature animals.

larger masses, and that if only a moderate number be introduced, hardly any disturbance of health will take place.

But perhaps the overwhelming number of parasites by which man is liable to be attacked will be best realised when we state that, in cases of the so-called "Cochin-China diarrhœa," the number of *Rhabditis stercoralis* which have been known to be evacuated in individual cases, within twenty-four hours, amounts to several hundred thousand or even to a million.[1]

Three points have to be noticed in regard to the way in which parasites affect their host. In the first place, they grow and breed at the expense of their host, from whom they thus abstract nutritive material. Secondly, they produce alterations in space as they press upon the surrounding tissues or obstruct the channels in which they live. Lastly, their movements, according to circumstances, may give rise to pain, to inflammation, varying in degree and in termination, or even to perforation and dissolution, — all which symptoms are, however, sometimes merely the result of continuous pressure.

The first of these three kinds of influence, although perhaps the one which occurs most frequently, is seldom of much pathological importance. There must be unusual influences at work, if the loss caused by the abstraction of nutritive material by the parasite for its metabolism, growth, and propagation is at all appreciable to the host, provided that he belong to the larger animals, and much exceed his parasites in size and nutritive requirements.

A *Bothriocephalus latus*, seven metres in length, weighs about 27·5 grms. According to Eschricht, it throws off yearly a number of pieces, which measure altogether about 15 to 20 metres, and may represent a weight of about 140 grms. Even on the supposition that the animal, which of course undergoes continuous metabolism, abstracts three or four times that quantity from its host,[2] and that the nutritive material consumed by all the parasites amounts to several pounds yearly, it is easy to see that so moderate a quantity is of hardly any account compared with the yearly consumption of the host. It is

[1] Normand, "Mém. sur la diarrhœ dite de Cochin-Chine," Paris, 1877, and Davaine, *loc. cit.*, 2d ed., p. 968.

[2] It does not require much proof to show that Heller's method of determining the host's loss of nutritive material simply by the bodily weight of the parasites is erroneous. (Art. "Darmschmarotzer" in "v. Ziemssen's Handb. d. sp. Path. u. Ther.," Bd. vii., Th. 2, p. 567; Eng. transl., "Cyclop. Pract. Med.," vol. vii., p. 678, London, 1877.) Moreover, there are some tape-worms whose growth is so rapid that Heller's method also would give extraordinary results. The tape-worm of the sheep, for example, which grows to the length of a hundred metres, has been found fifty-one metres long in lambs four weeks old.—Göze, "Versuch einer Naturgesch., u.s.w.," p. 371.

much the same in the case of the *Tæniæ*, and even of *Tænia saginata*, which throws off, let us say, eleven proglottides daily, with an average weight of 1·5 grms., and thus loses in the course of the year about 550 grms. of organic matter. If the number of parasites be greater, the association is of course more unfavourable. A female thread-worm, for example, produces, as we saw before, 42 grms. of egg-substance yearly; and taking into account what it requires for metabolism, must deprive its host during this time of at least 100 grms. Thus if, as sometimes occurs, there were 100 of them (there have been cases in which 1000 have been found at the same time in the intestine), they would cause a loss of 833 grms. monthly, which, under some circumstances, and especially in childhood, must have a very appreciable effect. Similarly, the 100,000 specimens of *Rhabditis stercoralis* (1 mm. long, 0·4 mm. in diameter) which are often evacuated daily by patients suffering from Cochin-China diarrhœa, represent by their mass alone—without [1] taking into account material used in metabolism—a weight of about 200 grms. And if it be considered further that the number of the evacuated worms may increase tenfold, it becomes easy to understand how a severe marasmus may ensue, even after a short illness.

I do not, however, cite these instances in support of the view that the disturbances of the nutritive functions, and their manifold external consequences, which the physicians were so willing to interpret as symptoms of helminthiasis, are always to be regarded as the direct consequences of the amount of nutritive material abstracted by parasites. Even if it be certain that the disease is connected with parasites, it is quite possible that the relation between disease and parasite is of an indirect nature, and brought about by the state of the infected organ.[2] Further, the continuance of any disease, however slight and partial at first, will affect the general conditions of the nutritive organs.

Nor is the nature of the materials which serve as nourishment to the parasites an unimportant factor in considering the effects of the association. Thus a blood-sucking parasite, *cæteris paribus*, causes a greater loss than one which feeds on epithelial cells. To this is due

[1] [As above mentioned (p. 46), these Rhabditidæ are the offspring of *Anguillula intestinalis*, which had been met with in the intestine by earlier observers, but whose genetic relation had remained unrecognised. Grassi and Perona have recently reported that they have found *Anguillula intestinalis* in patients suffering from catarrhal gastro-enteritis in Milan (*Archivio scienze medic.*, t. iii., No. 4, 1879).—R. L.]

[2] A very good example is afforded by the *Trichinæ*. In their wandering into the muscular tissue they not only destroy fibres, but, by paralyzing the muscles used in mastication and swallowing, they affect the introduction of nutriment to such a degree that within a very short time the patient experiences considerable atrophy.

the great clinical importance of *Dochmius duodenalis* (*Anchylostomum*, Dub.) (Fig. 10), which occurs in masses in man in many tropical and sub-tropical countries, and in the north of Italy, and is generally so full of blood that at first sight the intestine of the patient appears to be covered with leeches. As a rule, the presence of this worm soon produces an anæmic condition.[1] This disease, with many others resulting from it, is so common in Egypt, that nearly a quarter of the native population suffer from it (hence "*Chlorosis Ægyptiaca*"), and many perish for want of proper treatment, which ought of course, in the first place, to be directed towards the removal of these dangerous guests. In this case we have, of course, to consider not only the loss of blood which the parasites cause in filling their digestive apparatus, but that which results from the bleeding of wounds caused by their bites, which, according to Griesinger,[2] is often very considerable. It is in this way that even leeches may become dangerous, or even fatal, to man.

At this point it may also be mentioned that a very considerable loss of blood may be caused by the hæmaturia produced by the wandering of embryos, as in the case of *Filaria Bancrofti* (*F. sanguinis hominis*) and of *Distomum hæmatobium*.

But, on the whole, the disturbances resulting from the loss of strength, and interruption of the nutritive supplies, are considerably less than those which are occasioned by the growth and multiplication of the Helminths.

As soon as the worms exceed a certain size, they begin, like other foreign bodies, to exert a pressure on their surroundings, which increases with their size and with the inability of the surrounding structures to resist it. The influence of this pressure is, of course, most frequently felt in the case of the larger parasites, and especially in the case of those which have taken up their abode in narrow channels or in parenchymatous organs. The parts which are most immediately exposed to the pressure begin to lose their character and normal appearance at the points of contact with the foreign bodies. The canals must widen when the size of the inmates exceeds their normal diameter. They form sinuses, and, if the circumstances permit, even change into closed sacs, which become thicker and thicker through hypertrophy of the connective tissue, until they can

[1] In individual cases years may elapse before the disease breaks out in full vigour. The case of a workman in Vienna, who six years before had been a soldier in garrison in the north of Italy, led Henschl to suppose that *Dochmius duodenalis*, like the *D. trigonocephalus* of the dog, lives at first on epithelial cells, and only after they are exhausted betakes itself to the vascular connective tissue of the intestinal villi (*Mittheil. d. Vereins d. Aerzte in Niederösterreich.*, 1875).

[2] *Vierordt's Archiv f. physiol. Heilkunde*, Bd. xiii., p. 554, 1855.

hardly be distinguished from the cysts of the parenchyma-worms, which have been described (p. 19). The soft adjacent tissue begins at the same time to disappear,[1] and is finally completely destroyed, after more or less remarkable histological changes. We know, for instance, that the substance of the brain is gradually destroyed by the growth of the bladder-worm developing within it, and that the liver atrophies more and more in consequence of the ever-increasing pressure of *Echinococcus*, or of *Distomum hepaticum*, which inhabits the bile ducts.[2]

If the pressure of the growing parasites restrict the supply of blood to the infected organ, or in any other way affect its supply of nutriment, the destructive work will of course advance even more rapidly. In such cases the whole of the organ disappears, leaving hardly any traces of its existence. Thus, in animals whose kidneys are infected by *Eustrongylus gigas* the organ is ultimately only represented by insignificant sickle-shaped thickening (Fig. 76) surrounding the pelvis, which has been distended by the worm into a sac-like form.[3]

Further, even parasites of smaller size may, under certain circumstances, achieve the same results. The tiny embryos of the *Trichinæ*, for instance, soon cause disintegration of the sarcous elements of the muscular fibres which they perforate, so that the latter are transformed into granular sheaths. At first these sheaths have quite the same shape as the normal sarcolemma-sheaths; but afterwards, as the worms grow, an enlargement is formed around their resting-place, and this, after the disappearance of its ends and other changes, becomes a "*Trichina*-capsule" (Fig. 77).[4]

The eggs of parasites may produce the same effects as the worms themselves, if deposited in the interior of narrow channels, or in the parenchyma of the organs, as in the case of *Distomum* (*Bilharzia*) *hæmatobium*. The venous branches underlying the mucous membrane of the ureter in which this worm deposits its ova cause, through the

[1] Göze tells ("Versuch einer Naturgesch., u. s. w.," p. 234) of "a very lean and wretched looking" rat, of which the liver was so much riddled with Cysticerci that, "on account of the great number of bladders, hardly any of the tissue could be seen." Another very similar case is also given, *loc. cit.* p. 243.

[2] In this way the bile ducts of the rabbits are changed into more or less closed cysts, through the influence of the continuously developing and multiplying Psorospermiæ. A similar result may be observed in the Lieberkühnian glands of frogs, when infested by Nematodes and other parasites. According to Waldenburg (*Müller's Archiv f. Anat. u. Physiol.*, p. 195, 1862), the blood-vessels of the frog occasionally become worm-cysts, through aneurismal distention and sacculation.

[3] Hence earlier observers thought the seat of the worm was in the interior of the kidney.

[4] See Vol. II.; also Leuckart, "Untersuchungen über Trichina spiralis," 2d Ed., p. 53.

pressure of the foreign bodies which they contain, a more or less considerable hypertrophy in the surrounding tissue, and ultimately become so much altered, that hæmorrhage ensues, and they discharge their contents into the urinary passages. Similarly an active multiplication of cells has been observed to take place within the space where ova have been deposited by the Strongylidæ of the lung,[1] and round about the so-called " Psorospermiæ " (*Coccidium*, Leuckart), which have wandered into the epithelium. But the cells which are inhabited by the Psorospermiæ themselves are destroyed by the growth of the latter.

Fig. 76.—Kidney of *Nasua socialis*, with *Eustrongylus* in the distended pelvis.

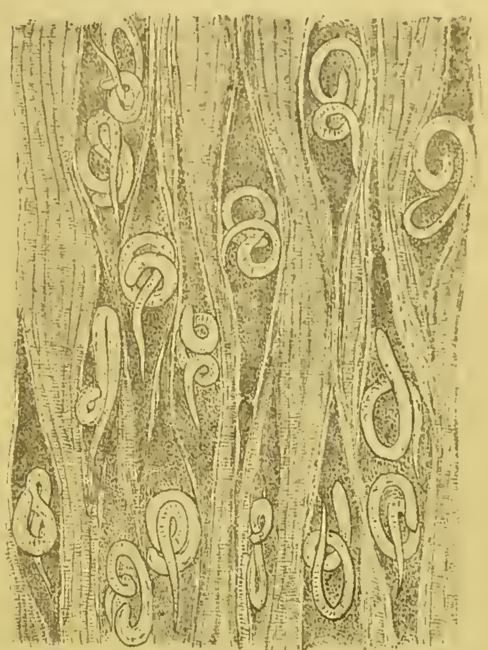


Fig. 77.—Muscle-*Trichinæ*, seven weeks old, in the distended sarcolemma-sheaths.

Such changes have, of course, an effect upon the functions of the infected organs. More or less serious disturbances arise, which affect the general health in various ways, according to their intensity, and the physiological importance of the invaded organ.

The parasitism of *Distomum hæmatobium* is followed by hæmaturia, and parasites in the brain give rise to imbecility, paralysis, madness, or convulsions, according to their situation.[2] Similarly, the

[1] Bollinger, "Zur Kenntniss der desquamativen und käsigen Pneumonie," *Archiv für exper. Pathologie u. Pharm.*, Bd. i., 1873.

[2] A very familiar example of this is afforded by sheep suffering from the disease called "staggers," caused by Cœnurus in the brain.—(See Numan, " Over den Veelkop-Blaasvorm der Hersenen," *Verhandl. koninkl. Nederl. Inst. Wetensch.* [3], Bd. iii., p. 225, 1850). The pressure exerted by the Cœnurus is often so great that, if the worm be in a peripheral position, even the bones become absorbed, and the neighbouring parts of the skull become quite flexible.

Echinococcus of the liver and the *Strongylus* of the kidney affect tissue metabolism by suppressing the biliary and urinary secretions; and the *Trichinæ*, by extensive destruction of muscular tissue, occasion more or less complete paralysis. This paralysis disappears some time after the infection, on account of a new formation of the muscular tissue, but no such renewal takes place after the destruction of liver or brain tissue, so that there the functional deviations are permanent, and often increase to such a degree that death is inevitable. It is true that in such cases the death of the host is not always the direct consequence of the first operations of the parasites, but often results from secondary disturbances; and among these, besides the cachexial and dropsical conditions often arising in the course of time from chronic ailments, the slow inflammations and dissolutions brought about by the irregular circulation, caused by the pressure on the larger blood-vessels, ought specially to be noted.

FIG. 78.—Ureter, with excrescences due to the presence of *Distomum*.

Fortunately cases of this description are rare. Most of the parenchyma-worms exert a less dangerous influence, and many, such as the *Cysticercus cellulosæ* of the muscles, cause hardly any disturbance. The result always depends upon circumstances, or, in other words, in such a case as the present, upon the amount of pressure exerted and the physiological importance of the affected organ. Thus the specific nature of the parasite is quite irrelevant, so that *Cysticercus cellulosæ*, for example, which we have just described as harmless when inhabiting the muscles, becomes a most dangerous parasite under certain circumstances and in certain situations, as in the brain or in the eye.

In wide spaces, where the parasites multiply into larger masses, their influence consists not so much in pressure as in a more or less complete obstruction of the passages. The influence of this obstruction on the health again depends principally on the relative importance of the organ in the economy of the organism. Thus the occurrence of *Cysticercus* in the anterior chamber of the eye, or in the vitreous humour, causes blindness. Similarly the aggregation of masses of worms (*Strongylus s. Syngamus trachealis*) in the windpipe of birds, and especially of our common fowls, often causes suffocation; and the intertwining of tape-worms and thread-worms in the human intestines produces conditions which have a great resemblance to intussusception of the intestine, or to strangulated hernia. If the interruption be not

so complete, the conditions produced naturally differ; but even when less serious, they often become fatal to the host through long continuance.

Perhaps it is well at this stage to note the so-called "worm-aneurisms," which are of such frequent occurrence in the mesenteric arteries (especially the anterior) of the horse that they can hardly be sought for in vain (according to Bollinger, only in 6 to 10 per cent.). There can be no doubt that these formations are caused by the parasitism of *Strongylus s. Sclerostomum equinum*, which, when quite small (p. 64), enters the intestinal canal of the horse from outside, but soon migrates thence into the circulatory system, and there gives rise to the formation of aneurismal sacs. The manner in which these aneurisms (Fig. 79) are gradually developed cannot be determined in the absence of the necessary data, but the general supposition is, that as soon as the worms reach the blood-vessels, they begin to bore into the arterial coats, and thereby cause a swelling and loosening of the walls, so that the lumen of the vessel is constricted, and the aneurismal enlargement produced.[1] It is true that afterwards the worms, which have now attained a length of 18 mm., are found chiefly among the masses of albumen in the aneurismal sac, but this situation is probably a secondary one. In some cases new aneurisms are formed in other parts by the wandering thither of the larger worms. That the existence of these aneurisms must often be followed by other diseases is very evident, from the fact that the anterior mesenteric artery in which they are usually situated is the source of blood for a long portion of the intestine, not less than 26 to 27 metres in length. It has indeed been proved by the researches of Bollinger[2] that the so-called colic of horses, which is

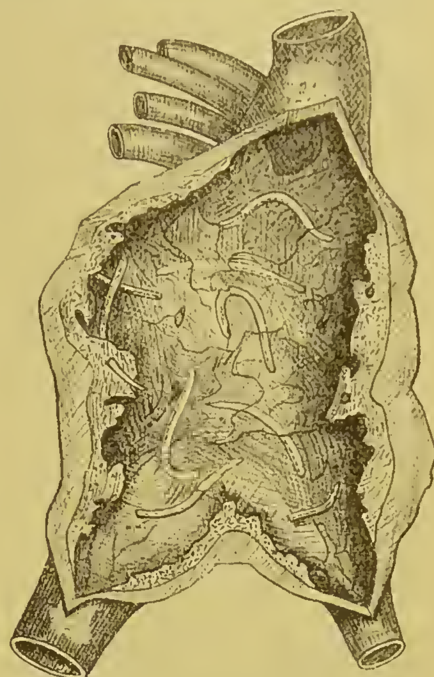


FIG. 79.—Worm aneurism of the horse.

[1] The supposition that the worms give rise to the aneurisms by means of their oral armature, rests upon complete ignorance of the circumstances of the case, since this oral armature is developed only shortly before the arrival of the parasites in the intestine—that is to say, when the pathological changes of the artery have long before been completed. See Vol. II.

[2] Bollinger, "Die Kolik der Pferde:" München, 1870.

so frequently fatal, is referable in most cases to embolic and thrombotic processes produced by worm-aneurisms.

Echinococcus may also give rise to emboli, especially when it perforates any of the larger venous branches, and empties its contents into them. The intruding bladders then generally obstruct the pulmonary artery, so that death rapidly ensues.

We have hitherto been considering only those influences of parasites on their hosts which are associated with their presence and growth. Very similar symptoms may occur under corresponding circumstances without the intervention of parasites; for instance, by the growth of tumours. Parasites, however, not only *grow*, but, with few exceptions, *move*, and this mobility, which distinguishes them so strikingly from neoplastic formations, becomes another source of manifold mischief to the harbouring organism.

Having already noted how the effects of the parasites differ according to their situation, size, and stage of development, it is easy to see at once that the disturbances caused by this mobility must be very various. It is evident, for instance, that the effects produced on the host must be very different when the parasites move about within a spacious abode, from those observed when they leave it, and wander through the body. The effects of these movements and wanderings also depend largely on the number and size of the animals, and upon the slowness or rapidity with which they are accomplished.

We shall therefore next consider the *modifications produced in the organism by the wanderings of the parasite within the body of the host.*

The case of the embryos first demands discussion. They are the most frequent wanderers of all, and, on account of their microscopic size, the most hidden; so that, without knowledge of their previous introduction, it is difficult to prove them to be the causes of disease. Such being the case, it is easy to see that their influence upon the host can be estimated in the first place only from the results of experiment. According to these, however, the effects have been found to be very far from trivial—supposing, of course, that the number of wandering embryos is not inconsiderable.

Fig. 80.—Embryo of *Tænia.*

For the purpose of introducing bladder-worms into Mammalia, I have been accustomed to feed several animals, and especially rabbits;[1] and in such cases it has often happened that the animal died in the course of the first few days, or even of the first twenty-four hours, without any obvious external cause. Since in such cases large quantities of the eggs of the tape-worm had been administered among

[1] "Blasenbandwürmer," p. 45.

the food, it is likely that death was caused by the wanderings of the embryos. In examining the carcase, the capillaries of the viscera were found considerably injected, especially in the lungs and liver, and sometimes even ecchymosis had resulted. The blood is also somewhat thin, but there are no other symptoms of any specific disease. Whether it may be supposed that the embryos (Fig. 80) have caused a capillary embolism in these organs by their wandering *en masse* into the circulatory system, I cannot decide, although I have succeeded in finding single embryos in the blood of the portal vein.

Similar cases have been observed by other investigators,[1] and one which Leisering describes, of a lamb fed with *Tænia marginata* (*e Cysticerco tenuicolli*), may be given here.[2] The principal changes in this animal, which died on the fifth day after feeding, were to be seen in the liver, which was congested throughout its whole extent, and traversed by enlargements of the portal capillaries, distended with blood, in which hundreds of small but yet visible tape-worm embryos were to be observed. Icterus and extravasations were also noticed, the latter even in the lungs.

It cannot be doubted that these were the results of the infection, although perhaps the direct cause of death cannot be established with certainty.

In cases in which the animals under experiment manage to survive the immediate consequences of the infection, and especially in cattle fed with *Tænia saginata*, a state is often produced, which in pathological and pathologico-anatomical respects has the greatest resemblance to miliary tuberculosis, and hence has been called by me "acute Cestodic tuberculosis."[3]

The Cestodes are not, however, the only parasites which influence their hosts by the wandering of their embryos. The movements of those of *Trichinæ* have also an influence; for the painful sensation of muscular exhaustion, which is felt even in the first days of trichinosis, and rapidly increases in intensity, the inflammation and œdematous swelling of the affected parts, and the restlessness and incipient fever, are all undoubtedly due in great measure to the condition of irritation produced by the wandering embryos. It must, however, be borne in mind, in considering the symptoms accompanying trichinosis, that this disease is the product of a whole series of helminthological conditions which run their course side by side in the same host, and

[1] See especially Raum, "Beiträge zur Entwickelungsgeschichte der Cysticercen:" Dorpat Inaug. Dissert., 1883.

[2] *Bericht über das Veterinärwesen Sachsens*, p. 22, 1857-58.

[3] Mosler, "Helminthologische Studien und Beobachtungen," Berlin, pp. 1 *et seq.*, 1864.

crowd themselves into so short a space of time that it is difficult to determine the effects of the individual factors. After a more copious infection in the case of pigs and rabbits, a more or less conspicuous reddening of the peritoneal covering of the intestine and the abdominal walls may often be observed within the second week, and sometimes even a matting together of the viscera, or a serous effusion into the body-cavity. All these phenomena, although not hitherto observed in man, can only be produced by embryonic wanderings. Virchow is of opinion that the typhoid conditions which accompany trichinosis may also be explained as the direct consequences of the wandering, but perhaps it would be nearer the truth to refer them to the absorption of the waste products, which are produced in masses by the destruction of the muscular tissue. It appears to me very doubtful whether the *Trichina*-embryos have any influence, as is supposed,[1] in virtue of certain inherent chemical properties.

Filaria Medinensis has also sometimes been accredited with poisonous properties, in order to explain the dangerous results which follow the tearing out of the worm; but it has been shown by the researches of Böttcher[2] that these symptoms are caused merely by the wandering of the embryos in countless numbers into the surrounding tissues, and that they are mainly of an inflammatory nature.

Similarly the embryos of *Strongylus filaria* hatched in the lungs of sheep and other ruminants frequently occasion a more or less extensive inflammation, which only ends favourably if the parasite obtain an exit. Very different from such general inflammations are the changes caused by the invasion of the embryos of *Ollulanus*,[3] which occur in the neighbourhood of each individual worm, and again present all the appearances of a miliary tuberculosis, and are no less dangerous than the Cestodic tuberculosis just mentioned.

Further, it is not so much the wanderings that act as causes of disease, as the irritations and injuries produced by them. This is most strikingly proved by the history of the so-called *Filaria sanguinis* (p. 50), which sometimes circulates in millions in the blood of its host, yet only causes disturbances when it gives rise to hæmorrhage in making its exit into the cellular tissue, or through the kidney, where it perforates the capillary tuft of the Malpighian body. The hæmaturia or chyluria which is caused in this way, and also that resulting from the operations of *Distomum*, if of long continuance, are followed by anæmic conditions, but this is generally the only expression of the helminthiasis.

[1] Friedreich, *Deutsches Archiv f. klin. Med.*, p. 265, 1872. Huber is of the same opinion in regard to *Ascaris lumbricoides*,—*Ibid.* p. 450, 1870.

[2] *Sitzungsb. der Dorpater Naturforschergesellsch.*, p. 275, 1871.

[3] See Bugnion and Stirling at the places mentioned on p. 47.

It is only in rare cases, according to Lewis, that the Hæmatozoa give rise to more or less serious disturbances in other organs through ruptures or capillary embolism. Gruby and Delafond have observed epileptic fits in dogs infected with these parasites.[1]

When the embryos have finished their wandering, and have settled down and begin to grow, new phenomena appear in place of the former ones, and are of greater or less importance according to circumstances. They have generally the character of local inflammatory affections, the causes of which are naturally found in the combination of the commencing pressure with the still slowly progressing motion.[2] The serious extent to which these inflammations may increase is shown not only by the instance we have given of acute Cestodic tuberculosis in the ox, but also by the constancy with which our experiments with Cœnurus produced in three weeks an inflammation in the brain of the sheep, which was usually fatal.[3] When the skull is opened in such cases, streaks of caseous exudation, about an inch in length, are seen on the surface of the brain (Fig. 81), marking out the path of the parasites and identified by the character of their surroundings as the centres of the inflammatory processes—(Haubner, Leuckart, van Beneden).

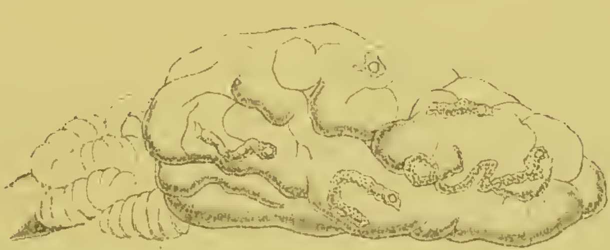


FIG. 81.—Brain of a lamb with tracks of Cœnurus.

These local phenomena are of course not equally dangerous in all organs. I have frequently seen the livers of rabbits which had been fed with *Tænia serrata* crossed and riddled by hundreds of young Cysticerci (Fig. 82, see also p. 70), and yet I do not remember a single case of death resulting from these disturbances.[4] As soon as the worms have slowly wandered out of the liver, that is to say in the

[1] *Comptes rendus*, t. xxxiv., p. 9, 1852.

[2] There is no doubt that the continuous pressure of the growing worm often of itself gives rise to inflammatory processes; so that it is sometimes impossible sharply to distinguish the effects of simple pressure from those caused by the motion of the parasites.

[3] This inflammation of the brain is somewhat incorrectly called "staggers" by some investigators, but the characteristic symptoms of the latter disease do not appear until some months after infection.

[4] Compare with this the plates in my work "Blasenbandwürmer," p. 124, Part i., Figs. 1-3.

third or fourth week after they have been administered to the animal, the passages which they have made close up. The former congested condition then ceases, the exuded material which, along with the worms, had blocked the passages is reabsorbed, and a healthy appearance returns. Only the persisting scars betray the former state of the organ.

I have found it to be the same in the case of *Cysticercus tenuicollis*, except that, as this is of larger size at the time of its exit, it may under similar circumstances produce more serious effects. In livers

Fig. 82.—A piece of the liver of the rabbit with perforations caused by bladder-worm (*Cysticercus pisiformis*).

Fig. 83.—Exit of a young *Cysticercus tenuicollis* from the liver.

which had just been left by these parasites, I have seen holes so long that the finger could be inserted nearly half-an-inch. The healthy state of my animals is explained by the fact that the number of parasites was not very large, never indeed above twelve. The emigration of a greater number produces not seldom, however, fatal effects.

Much more dangerous are the consequences of the repeated wanderings of *Pentastomum denticulatum* (see p. 77) from the liver and lungs. In order to understand this, it is only necessary to see the rapid and powerful leech-like motions of the animal and its armature, consisting of circles of hard bristles and the powerful hooks (Fig. 56). After a copious infection, the liver and lungs are perforated in all directions, and their surfaces are covered with holes (Fig. 84), each of which forms the centre of a more or less extensive inflammatory circle. This is especially the case in the lungs, which are often greatly distended by infiltration of blood and exuded fluids. When the *Pentastoma* migrate in larger numbers into the cavity of the body, these symptoms are usually accompanied by peritonitis, which frequently terminates fatally.[1] Even cases of natural infection may be followed by fatal results, as is proved by the instance which Weinland gives of

[1] Leuckart, "Bau und Entwicklungsgesch. von Pentastomum tænioides," p. 14, Leipzig, 1865.

an *Antilope bubalis* which succumbed to *Pentastomum denticulatum.*[1] Still we have not yet observed any case of *Pentastomum* becoming dangerous to man. This is probably due to the fact that as the usual mode of transference is the smelling and licking of the hands by dogs, it is imported singly or in very small numbers. *Pentastomum constrictum* (Fig. 85 *A*), which infests man in the tropical regions of Africa, seems on the other hand to have a much more intense influence on its host, for

FIG. 84.—Lung of a rabbit infected with *Pentastomum.*

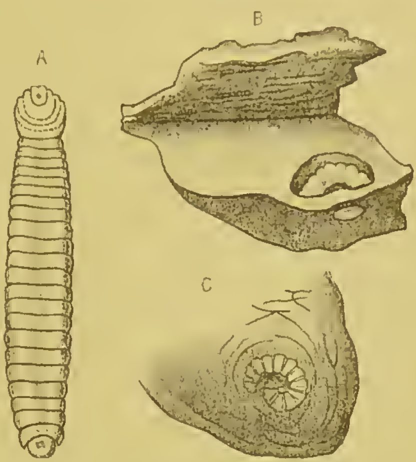


FIG. 85.—*Pentastomum constrictum*; *A*, twice natural size; *B*, liver (after Aitken); *C*, in the lung.

according to the information furnished by Aitken[2] in regard to a few cases of this kind, the exit of this parasite from the liver and lungs frequently causes death.[3] It must, of course, be remembered that while the length of *P. denticulatum* is hardly a centimetre that of *P. constrictum* is nearly seven.

We have hitherto considered only those wanderings which occur constantly and regularly in certain parasites, and sooner or later in their developmental life. The number of cases cited would have been greater if we had not turned our attention exclusively to the higher animals. Otherwise, we should have mentioned the almost always fatal wanderings of the parasitic larvæ of various insects and *Filariæ* (*Gordius, Mermis*).[4] But without these, the account which has been

[1] *Der zoologische Garten*, p. 2, 1860.

[2] On the occurrence of *Pentastomum constrictum* in the human body as a cause of painful disease and death: Aitken, "The Science and Practice of Medicine," 4th ed., 1866.

[3] Wedl (*Sitzungsb. d. k. Akad. Wiss. Wien*, Bd. xlviii., p. 408, 1863) mentions a similar case of a lioness which contained a large-sized *Pentastomum* (*P. moniliforme* ?) in its liver and spleen.

[4] Of the other cases belonging to this class, I shall only cite an observation made by Busch ("Beobachtungen über Anatomie und Entwicklung wirbelloser Seethiere," p. 98, Berlin, 1851) regarding a small asexual Nematode, which perforates the tissues of the

given is sufficient to establish the pathological importance of these phenomena.

Besides the constant and regular wanderings of the larvæ, there are similar movements associated with the full-grown animals, but these are, as a rule, only occasional and fortuitous. Among them we class those of *Ascaris* into the body-cavity, which, of course, presuppose perforation of the alimentary canal.

The possibility of such perforations has been much questioned, both in earlier and more recent times, because the thread-worms are without any kind of boring apparatus. It has also been attempted to explain the numerous cases of this kind mentioned in literature by the supposition that the worms play only a secondary part, since they have been observed, perhaps after the death of the host, to make use in their movements of passages caused by ulcers perforating the intestine. In proof of the correctness of this hypothesis the character of the perforation has been cited, which seems to be the result rather of a gradual erosion than of a mechanical force.

Although it is difficult to decide the question with certainty, I think that the denial of the presence of these perforations is quite unfounded.[1] That a boring apparatus is by no means necessary for the perforation of tissues and organs has been decided by modern investigations, and is indeed sufficiently proved by the instances which we have collected of wandering Cysticerci. When we consider the size of these thread-worms, it is, however, evident that they cannot perforate the walls of the intestine with the same ease as the embryos of *Trichina.* If the boring of the latter be described as an "acute" process, that of *Ascaris* might be termed "chronic," since it is accomplished by means of a continuous pressure of the head against the wall, a process perhaps resulting not directly in a perforation, but, in the first place, only in certain structural changes in the tissue, which then in turn make the perforation possible.

In some cases the perforation is not confined to the wall of the intestine. At the umbilicus, and in the inguinal regions, where the abdominal wall yields more easily to pressure, not only the intestine but also the body-wall is perforated. In consequence of the pressure exerted by the parasite, the so-called "worm-abscesses" arise, and inflammation of the connective tissue, which is eventually followed by ulceration, exactly as in the case of the perforations due to *Filaria Medinensis.*

Sagittæ indiscriminately in all directions. "The poor *Sagittæ,*" he says, "of course suffer terribly when the invaders begin their wanderings, and generally die in a tetanic condition, with the hooks stretched out stiffly from the head, and the body bent rigidly backwards."

[1] See Vol. II.

It is self-evident that the consequences of such boring out of or into the body-cavity must be much more deep-seated and dangerous than those which result from the mere wandering of an embryo. The size and very appreciable movements of the parasite usually produce in man a very intense peritonitis, which has a specially rapid and fatal course in those cases in which other foreign substances have passed through the walls of the intestine along with the worms.

Thread-worms, however, are not the only intestinal worms which are capable of such migrations. These are even more frequently undertaken by the Acanthocephali, which, with their powerful hooks studding the sides of a retractile proboscis, are specially adapted for such work. Even the *Echinorhynchus gigas* of the pig, although several millimetres in diameter, can by means of its boring apparatus perforate the walls of the intestine. We know also of similar wanderings, even among the tape-worms—not only in the case of *Tænia solium*, but also of other species not provided with hooks. Thus *Tænia plicata* not unfrequently passes from the alimentary tract of the hare or rabbit to the body-cavity, without, however, exciting the usual serious symptoms, since these hosts are but slightly liable to peritonitis. Göze found in one case[1] "a small aperture closed by thickened margins, by which the worms had made their exit, and which could only be observed internally on the villous surface." He further cites the case of a diver infested with *Ligula*, some of which had penetrated the intestinal walls.[2] In its larval state the *Ligula*, as is well known, inhabits the body-cavity of white-fish, especially of the bream, and towards the end of August it often breaks through the body-wall "ventrally, laterally, or dorsally, or even sometimes on the head or near the tail. The point where the perforation has taken place is somewhat swollen, the skin becomes thin, and the blood-covered wound which is left is longitudinal, like that of an artery."[3] Steenstrup observed a similar phenomenon in the *Schistocephalus* of the stickleback, but in this case the injury generally proved fatal.[4]

In contrast to these only occasional wanderers, there are also adult parasites which are continually moving. Chief among these is the itch-mite (*Sarcoptes scabiei*), which burrows in all directions in the epidermis (Figs. 86 and 87), and by the perforation of the papillæ of the cutis causes the painful eruptions which were for many centuries considered as a special disease—the itch.

[1] "Versuch einer Naturgesch., u.s.w.," p. 367.

[2] *Ibid.*, p. 25 and p. 185.

[3] Bloch, "Abhandl. u. s. w.," p. 2.

[4] See the observations cited on page 25, and also v. Baer, "Ueber Linnés im Wasser gefundene Bandwürmer," *Verhandl. naturf. Freunde Berlin*, Bd. i., p. 388, 1829.

The species of *Filaria* which infest the connective tissue of their host are similar in habit to the itch-mites. They have been usually, but erroneously, regarded as quiescent Entozoa, while in reality they are in constant, though slow, motion. And since many nerves and blood-vessels ramify in this connective tissue, it is on *a priori* grounds probable that these parasites are the cause of many pathological phenomena.[1] These will of course vary widely in detail, according to special conditions, but will especially depend on the nature of the organ attacked and the character of the wandering parasite. Thus *Filaria Medinensis* moving among the muscles gives

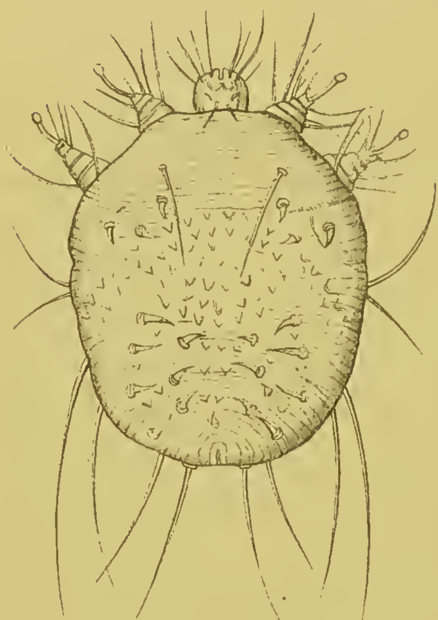


FIG. 86.—*Sarcoptes scabiei.*

FIG. 87.—Crust of *Scabies norvegica*, with mites, their borings, eggs, and excreta.

rise usually only to a more or less violent pain, while *Filaria loa*[2] under the conjunction of the eye causes a chronic inflammation, and *Filaria Bancrofti*, the parent of the *Filaria sanguinis* (p. 50), discovered by Lewis, inhabiting the sub-epidermal tissue, especially in the inguinal region, causes sclerotic and lymphatic changes, which have a

[1] Eisig observed a *Filaria* in the kangaroo, which had bored through the pericardium, and thereby induced a fatal pericarditis.—*Zeitschr. f. wiss. Zool.*, p. 99, Bd. xx., 1870.

[2] Through the kindness of Dr. Falkenstein, a member of the German-African expedition, I have had the opportunity of examining a specimen of *Filaria loa*, and have convinced myself that it is by no means identical with *F. Medinensis*, but differs widely from that form. The embryos enclosed in thin egg-shells bear a close resemblance to *F. sanguinis*, but are smaller (0·21 mm.).

certain resemblance to elephantiasis, and have been often regarded as such.[1]

Under such circumstances, it is not surprising to learn that worms by their movements frequently cause disturbance, and often very serious disturbance, in the intestine and other viscera. They excite irritation, which in delicate lining membranes naturally leads to catarrhal and inflammatory states proportionate in intensity to the number and activity of the parasites.

A striking proof of the correctness of this statement is furnished by the *Trichinæ,* which immediately after their introduction give rise to a series of pathological phenomena in the intestine,[2] which, in cases where the parasite is abundant, are so intense that the patient sometimes appears as if attacked by cholera. In rabbits and other small animals death not unfrequently supervenes at this stage. On dissection the intestine is seen to be strongly injected, and the mucous membrane is covered by a thick layer of dead epithelial cells, forming, as it were, a false membrane. In the same way it has been found that the so-called "Cochin-China diarrhœa" (which we had the first opportunity of studying closely only a few years ago, through the French soldiers who suffered from it) is determined by a small parasitic thread-worm (*Anguillula intestinalis*), and its Rhabditiform embryos, which in incredible numbers infest the intestine throughout its whole length, from the stomach downwards, and even fill the ducts of the associated glands. Many thousands of these worms are voided at each stool, while the *Trichinæ,* on the contrary, which live between the villi, are but rarely expelled. The voided worms are, however, continuously replaced, and hence a state of anæmia soon ensues; and it is this which, in spite of the continual diarrhœa, keeps the intestine from exhibiting signs of congestion. One of the common thread-worms, the so-called "maw-worm" (*Oxyuris vermicularis*), also occurs sometimes in great numbers, and then it not unfrequently happens that mucus and even bloody diarrhœtic stools result.

Nor do thread-worms only occasion such intestinal phenomena when they occur in great numbers, but tape-worms may do so likewise. In proof of this assertion, I may refer to the fact that the intestine of the dog, so generally infested by *Tænia echinococcus* or *T. cucumerina,* exhibits, as far as the worms extend, a loosened and reddened mucous

[1] Here we might also cite the case of *Stephanurus dentatus* (= *Sclerostomum pinguicola*), which occurs very abundantly in swine in North America and Australia. It inhabits the fatty masses near the kidneys, and riddles them in all directions, producing cavities filled with pus (see p. 46). The affected swine suffer pretty constantly from paraplegia.

[2] The existence of these intestinal affections was for a while emphatically disputed by Virchow, Knoch, Zenker, and others, until the epidemics at Hettstädt, and especially at Hedersleben, established my observations beyond cavil.

membrane; and these structural changes cannot be without correlative influence on the intestines. I have further established by experiment that tape-worms may under some circumstances prove fatal. I fed a dog with about 150 pieces of immature *Tænia cœnurus*, each piece about a span long, and forming altogether a bolus about the size of a goose's egg. This I thrust into the animal's pharynx, beyond the root of the tongue, in the hope that these worms would at least partially develop further in their new host. This did not happen, for eighteen hours after the feeding the powerful dog was a carcase. On examination, the stomach and duodenum were found to be filled with a bloody fluid. The walls were very strongly injected, covered with abundant ecchymoses, and partly with a loose layer of altered epithelial cells. The same phenomena, in a less conspicuous degree, could be traced to about the middle of the small intestine. The tape-worms were entirely digested, but traces of them were discoverable here and there in the small intestine; yet I do not doubt that they were to blame for the death of the dog, and would hazard the suggestion that this was due to the rapid and violent movements of the worms in their endeavour to escape the fatal action of the digestive juices. At any rate, the common supposition that tape-worms are among the slowest and most indolent of organisms is certainly erroneous, as any one may satisfy himself by observing them in their natural environment, the warm intestine, or even in a hatching apparatus.

But the presence of a great number of intestinal worms is by no means a necessary antecedent to such pathological changes. Even a single tape-worm or *Ascaris* can determine a more or less intense intestinal irritation, provided only that it be habitually characterised by a somewhat vigorous motion. I have frequently observed a reddening and loosening of the mucous membrane, like that we have cited as produced by *Tænia echinococcus* and *T. cucumerina*, in cases where only a single large tape-worm or thread-worm was present, and the pathological condition was so strictly limited to the area occupied by the parasite that there could be no doubt as to the causal relation.[1] Since the dissection was made immediately after death, the result could be no *post mortem* phenomenon, but could only be referred to the movements of the living worm.

A state of intense inflammation is sometimes excited by parasitic

[1] Here might be quoted the following observation of Göze (see *loc. cit.*, p. 71):—"My child suddenly died on the 11th February 1778, and on *post mortem* examination on the following day there was found in the intestine, not far from the stomach, a large thread-worm, which had caused a red inflammatory spot at the place where it had lain."

insect larvæ.[1] The symptoms of such states vary according to the condition and individuality of the patient, but the most frequent are disturbances of some sort in the digestive function, or perhaps the colic-like pains consequent upon these. The presence of larvæ of *Anthomyia* sometimes results in symptoms not unlike those of cholera. In many cases the phenomena are further complicated by the irritation of the sympathetic and reflex systems of nerves, and thus arise convulsions—sometimes local, sometimes general—St. Vitus' dance, and similar troubles. Many exaggerated statements may have been made upon this matter, but we have no right on that account to deny the existence of a relation which numerous observations have made in the highest degree probable, and which involves no inconsistency with anything that we know of the nature of these diseases.[2]

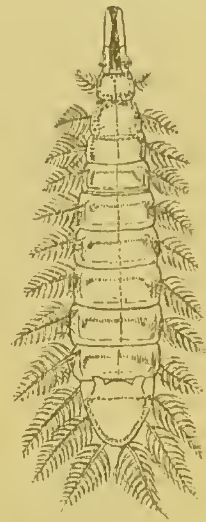


Fig. 88.—Larva of *Anthomyia cunicularis.*

What has been said here of intestinal worms is also essentially true of the inmates of other organs. Congestion and inflammation, with their manifold secondary consequences, are ever the first results of the irritation caused by the various parasites.

A most familiar example is furnished by the species of *Strongylus* which often occur in great numbers in the bronchi of ungulates (*S. micrurus* and *S. rufescens* in the ox, *S. filaria* in the sheep, *S. paradoxus* in the pig). These excite inflammation, which spreads rapidly from the affected bronchi to the associated pulmonary tissue, and often ends fatally. *Filaroides mustelarum* (= *Spiroptera nasicola*, Leuckart), living in the frontal sinuses, causes the absorption of the walls outwards to

[1] Of the numerous relevant observations I will only cite one: Meschede, "Fall von plötzlicher schwerer Erkrankung durch verschluckte Fliegenmaden."—*Virchow's Archiv f. pathol. Anat.*, Bd. xxvi., p. 300, 1866.

[2] I may take this opportunity of citing the "odd observation" which Göze (*loc. cit.*, p. 27, note) made on a young dog, hardly one year old, which suffered from *Tænia cucumerina*. "He was often seized with cramp, caused probably by the number of the worms, and lay with his head and back bent, and the belly uppermost. He bent often to the side, and rolled himself on the sand, but during the whole period of two months that I watched him I never heard him bark once. I then administered a drastic purgative, which led to the expulsion of a whole bowl of tape-worms, with and without 'heads.' He was restored to health, and began to bark next day. Are there not instances of children infested with worms remaining deaf and dumb for years? I recall at least the title of a dissertation—'De aphonia ex vermibus.'" Similarly Leisering remarks, on the strength of his own observation, that dogs much infested with *Tænia echinococcus* not unfrequently suffer from a disease exactly like hydrophobia in its external characters (*Bericht Veterinärwesen Sachsens*, Jahrg. x., p. 87, 1864).

the periosteum, and thus riddles the skull.[1] Similarly, *Pentastomum tænioides*, parasitic in the nasal cavity of the dog, occasions after some time (according to Chabert) distinct caries. In recently infected animals an injection and loosening of the Schneiderian membrane is all that can be observed. The effect of *Pentastomum* upon the lungs is much more serious. I have already mentioned how, in a snake (*Naja haje*) which I examined, it was evident even to the naked eye that death had resulted from pneumonia caused by *Pentastomum*. There were numerous inflamed regions in the lungs as large as the palm of the hand, and bearing in their centre a *Pentastomum* firmly fixed by its hooklets.

Even the horseleech (*Hæmopis vorax*), in tropical countries, and especially in North Africa, is sometimes the cause of chronic inflammation in aggravated cases of laryngeal consumption, which occurs when the animal is inadvertently swallowed by man or beast when drinking, and settles in the throat or larynx. Still more acute and serious are the attacks made by the larvæ of *Musca* (*Lucilia*) *hominivorax* on the throat and nasal cavities of their unfortunate host. Vercamer, a Belgian army surgeon, reports of a soldier in Mexico that in a short time these animals had, with their oral hooks, eroded the glottis, and so riddled and torn the pillars of the fauces and the soft palate, that they looked "as if they had been stamped by a punch."—(van Beneden.) Even in our own country the physician has often the opportunity of observing the mischief wrought by insect larvæ, especially *Musca vomitoria* (Fig. 89) and *Sarcophaga carnaria*, parasitic in cases of neglected wounds or blennorrhœa. The abscesses caused in tropical countries, and especially in America, by the gad-fly and chigoe, are worth mentioning as analogous phenomena.

Fig. 89.—Larva of *Musca vomitoria*. (Nat. size and enlarged.)

Perhaps we should also mention here the repeatedly observed case of horses, in which the skin, covered with a herpetic eruption, was literally inhabited by larval Nematodes.[2] Another problematical

[1] See Weijenberg, *Archives néerlandaises sci. exact. et nat.*, t. iii., p. 428, 1868.

[2] See cases cited by Rivolta, *Il medico veterinario Torino*, p. 300, 1868; or Hering's *Repertor. f. Thierheilk.*, Jahrg. xxix., p. 373, and Sommer, *Oesterr. Vierteljahrsschrift f. Veterinärkunde*, Bd. xxxiv., p. 183.

case is reported by O'Neill[1] from the West Coast of Africa, where a skin disease resembling itch occurs among the negroes, and is also attributed to the presence of young Nematodes. I have myself had the opportunity of confirming the existence of such parasites on the skin of a diseased fox, but am still doubtful whether the disease can be called parasitic; and I have been confirmed in this doubt by finding, among the scabs of the eczematous skin of a dog, numerous flea-larvæ, which could hardly have produced the eruption, but had probably only taken advantage of it as an abundant source of food.

Glancing over the various pathological states induced in manifold ways by our unbidden guests, we survey a long catalogue of affections of most varied nature and importance. It is but rarely, however, that they show a combination of features so specific and characteristic that one can at once and with probability decide as to their nature and etiology. On the contrary, the results of parasitism might, in the majority of cases, be referred quite as well to entirely different causes.

DIAGNOSIS.

Such being the case, it is evident that a sure diagnosis of helminthic diseases necessitates, in the majority of cases, an objective proof of the existence of the parasites.

This proof may be furnished in various ways, according to the occurrence and nature of the parasites. It is most readily forthcoming, if we omit the Epizoa from consideration, in the case of those which inhabit the alimentary canal, or other organs opening to the exterior, not only because the animals frequently pass out of themselves, or are expelled by proper treatment, but also because, with few exceptions, they are sexually mature, and produce eggs in such immense quantities that their detection in the excreta by the aid of the microscope is a matter of very little difficulty. The importance of the examination of human excrement has been already emphasised on all hands, especially by Davaine,[2] Lambl,[3] and Vix,[4] and even earlier by Malmsten and others.

Among the Helminths infesting man there are (including *Dochmius*) nine species which have to be considered in such examinations:—

Three Cestodes—
Tænia saginata (Fig. 90, *H*).
„ *solium* (*I*).
Bothriocephalus latus (*K*).

[1] *Lancet*, Feb. 1878.
[2] *Mém. soc. biol.*, t. iv., p. 188, 1857.
[3] *Prager Vierteljahrsschrift*, Bd. i., p. 1, 1859.
[4] *Allgemeine Zeitschr. f. Psychiatrie*, p. 114, 1860.

Two Trematodes[1]—

Distomum hepaticum (*F*).

" *lanceolatum* (*G*).

Four Nematodes—

Ascaris lumbricoides (*A*).

Oxyuris vermicularis (*B*, *C*).

Trichocephalus dispar (*D*).

Dochmius duodenalis (*E*).

They all produce eggs of such characteristic form and size (see figure), that one can, almost by a mere superficial inspection, refer them to their parent animal. The eggs of the two species of *Tænia*

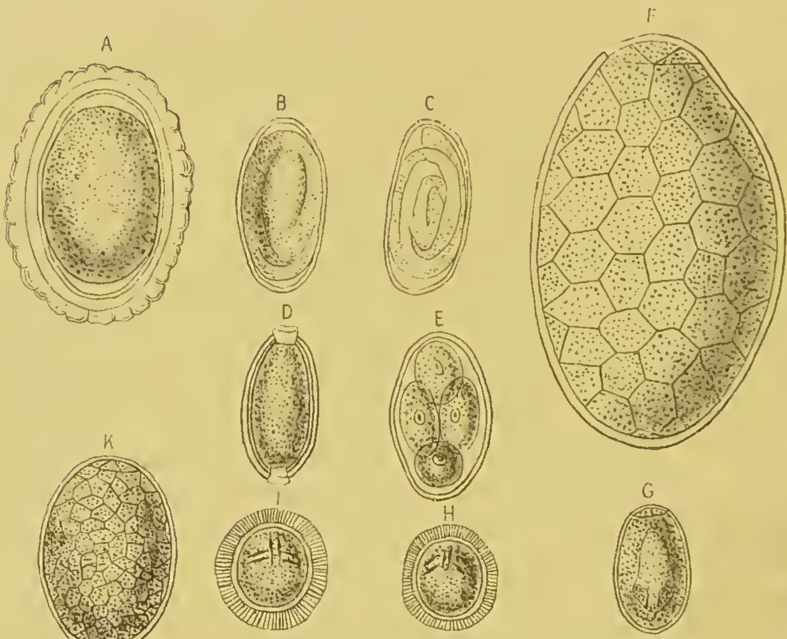


Fig. 90.—Eggs of worms found in the alimentary canal of man. (× 400.) *A*, *Ascaris lumbricoides*; *B*, *C*, *Oxyuris vermicularis*; *D*, *Trichocephalus dispar*; *E*, *Dochmius duodenalis*; *F*, *Distomum hepaticum*; *G*, *Distomum lanceolatum*; *H*, *Tænia solium*; *I*, *Tænia saginata*; *K*, *Bothriocephalus latus*.

are the most difficult to distinguish. They differ almost solely in that those of *T. solium* are somewhat more spherical, and on the whole smaller, than those of *T. saginata*. The eggs of *Distomum hepaticum* are the largest, and indeed gigantic, attaining a size of 0·135 mm. long by 0·083 mm. broad. They are nearly twice as long as the eggs of *Bothriocephalus latus* and *Ascaris lumbricoides*, and

[1] These both live in the gall-ducts, out of which the eggs are only accidentally transferred to the alimentary canal.

thrice as long as the others. Like the eggs of *Distomum lanceolatum* and *Bothriocephalus,* they bear a small, usually inconspicuous, lid at one end. The eggs of the two species of *Tænia* are provided with an extremely thick shell, the more conspicuous since it has a brown colour and distinct radial markings, caused by a covering of closely packed little rods. The eggs of *Ascaris lumbricoides* and *Trichocephalus dispar* are also thick-shelled, and the former are further enveloped in an albuminous sheath, usually coloured with bile pigment, while the latter are perforated at the poles and provided with an albuminous plug. The contents of the eggs also vary, being sometimes, indeed usually, unaltered, but sometimes in process of yelk-division (*Dochmius*), or even already exhibiting an embryo, as in *Tænia solum, T. saginata,* and *Oxyuris.* In the last instance the embryo is only partially developed.

We can to a certain extent infer the proportionate number of the different parent parasites from the quantity of eggs expelled from the host, but in so doing we must remember that the fertility of the various forms is by no means equal. And further, the eggs will be more easily and more abundantly found the nearer the parasite is to the anus, for then they will not be indifferently mixed through the fæces, but will be found especially in the outer portion and mucous surroundings. The eggs of *Oxyuris* are most easily demonstrated. This statement is consistent with the result of Vix, who among his patients affected with *Oxyuris* never found a single case where the eggs were not to be observed in countless numbers in the first microscopic preparation, or even first field of vision. Vix recommends further the examination not of the fæces, but only of the mucus, which can be easily removed from the anus or higher portion of the rectum with the handle of a scalpel or catheter. This method might suffice for *Oxyuris,* but is less likely to succeed in the case of other parasites which infest higher portions of the alimentary canal, and whose eggs are chiefly found in the fæces themselves. Therefore, in suspected cases of helminthiasis, the fæces ought not to be left unexamined, even when the examination of the mucus yields no positive result.

We need not further discuss the methods of examination, since these will partly suggest themselves in the course of what is certainly not a very pleasant task.

It ought, however, to be specially noted that in some established cases of *Tænia* the eggs are sought for in vain. This is readily intelligible when we remember what we have previously (p. 65) mentioned, that the eggs of these animals are not liberated within the alimentary canal, but reach the exterior still enclosed in the proglottides. The eggs which, in spite of this, are found here and there in the fæces,

arise from an accidental rupture of the joint, often readily consequent on the contraction of a distended uterus. One does not expect to find eggs of *Trichinæ* on such examination, since, as is well known, the embryos of these worms become free within the body of the parent, and immediately bore through the walls of the intestine. But, on the other hand, one sometimes finds the mother-*Trichinæ* themselves, though on the whole much less frequently than, judging from the analogy of *Rhabditis stercoralis*, one would expect from their usually very abundant occurrence in the alimentary canal of the host. To understand this we must remember that the *Trichinæ* are enabled by their long, thin form to adhere closely to the intestinal villi, and, thus protected, to escape the pressure of the fæces.

Balantidium (*Paramœcium*) *coli* is, like *Rhabditis stercoralis*, also to be found in great abundance in the fæces and intestinal mucus both of man and of the pig. In similar fashion evidently we may expect to diagnose *Strongylus gigas*, *Filaria sanguinis*, and *Distomum hæmatobium* from the urinary deposits, the species of *Strongylus* infesting the air passages from the sputum, and *Pentastomum tænioides* from the nasal mucus; and all this has been at least partially established by experiment.

The inmates of the various organs which open to the exterior are not, however, the only parasites whose presence admits of objective proof. Thus by the simple examination of the tongue, especially of the under surface, it is sometimes possible to affirm the presence both of *Trichinæ* [1] and of Cysticercus.[2] Similarly we can, by the use of the opthalmoscope, not only recognise the same inmates in the eye, but determine their position with the greatest accuracy.[3] When the suspicion of trichinosis is not fully confirmed by the usual methods, we have only to remove a small piece of flesh from the deltoid, or from any other easily accessible muscle, and subject it to microscopic examination.

Filaria Medinensis presents no peculiar difficulty in diagnosis, especially in the later stages, when the head of the worm has bored through the skin, and when the living brood passes to the exterior along with the secretion of the perforated part. The diagnosis of Cysticerus in the intermuscular connective tissue is less certain, for

[1] This is only possible when the *Trichina*-capsules are already calcified—that is to say, when the infection had occurred some considerable time previously.

[2] Even Aristotle recommends the examination of the tongue in pigs for the diagnosis of bladder-worm disease ("Hist. anim.," lib. viii., cap. 21, N. 3, "Δῆλαι δ᾽εἰσὶν αἱ χαλαζῶσαι· ἔν τε γὰρ τῆς γλώττης τῷ, κάτῳ, ἔχουσι μάλιστα τὰς χαλάζας."

[3] See especially the observations of v. Gräffe, *Journal f. Ophthalmologie*, p. 308, 1857. According to a later report (*Verhandl. d. med. Gesellsch. Berlin*, p. 96, 1871), v. Gräffe has observed more than a hundred cases of bladder-worm in the eye.

the cysts which may be felt through the skin might be mistaken for abscesses or other tumours. In many cases, however, a sufficient and reliable diagnosis may be based on the manner of occurrence and distribution, but only the results of excision and puncture can finally establish the diagnosis, and this corroboration ought never to be dispensed with if the detection of the evil is of any use, as, for example, in the case of contemporaneously occurring mental diseases.

Among the remaining parenchyma-worms it is sometimes possible to distinguish *Echinococcus*, and that not only when, as occasionally happens, it empties its contents through the lungs or kidneys, or the alimentary canal, but also when it remains quiescent in the form of a closed cyst. A diagnosis may then be established by means of auscultation and percussion. We are thus not only informed of the existence of an encysted tremulous swelling, but by means of the so-called "hydatid sound" are enabled to identify it as a specific formation, and to distinguish it from other dropsical swellings.

CURE AND PREVENTION.

After the detection of a parasitic disease there must follow, not only a treatment of the various symptoms, but a realisation of the *indicatio causalis*; that is to say, the removal of the parasites whose presence has induced the pathological state.

The means taken by the physician to attain this end will, of course, vary greatly, according to circumstances, and will not in every instance lead with equal ease to the desired result. In general, the more accessible the organ which the parasite infests, the more hopefully may success be looked for.

The simplest problem is evidently the removal of the Epizoa, either directly by mechanical means, or, more thoroughly and conveniently, by killing them with suitable preparations (mercury, ethereal oils, petroleum, &c.). In general, the inmates of the alimentary canal stand next as regards facility of expulsion, although the varied structure of the organs of attachment occasions considerable differences in matters of detail. These worms are treated with the so-called "anthelmintics," in which our pharmacopæia so richly abounds. Their action is primarily directed either against the worms themselves or upon the walls of the alimentary canal. The majority of specific worm-cures belong to the first class. They operate by killing or stupefying, or in some way unpleasantly affecting, the worms, so as to induce them to wander outwards, while the second class are successful by increasing the peristaltic movements, or by altering the secretions.

We restrict ourselves here to mere hints, for our knowledge of the real nature of the operations of these anthelmintic remedies is still uncertain and fragmentary. The experiments of Küchenmeister—who (following Redi's example) brought *Ascaris* and other intestinal worms into direct contact with certain substances—have done, as yet, but little to enlighten us upon this dark subject, though they deserve full recognition as the first attempts made to settle the question in a rational manner.

In the other vegetative organs, worms can generally be treated only indirectly, by applications which increase the functional activity of the structure affected, and especially increase its secretions. Success can only be doubtful, though the hope is that the worms will be carried to the exterior with the copiously flowing secretion. It is of course presupposed that the parasites are not of any considerable size; for, in such a case, an alteration in the functional activity of the surrounding organ could at most induce the inmate to make a spontaneous emigration.

As to worms occurring in the parenchyma, the healing art can only avail when they occur in superficial organs, and then only operatively. Thus, the well-known *Filaria Medinensis* may be gradually wound out from the sub-epidermal tissue, and the bladder-worm may be extracted from the eye (as has lately been done repeatedly, especially by von Gräffe) like cataract. We know, too, of numerous instances where *Echinococcus* has been removed from the liver and other internal organs by a fortunate operation, such as opening the cyst by means of caustic paste, by the application of electricity after previous puncture, by injection of tincture of iodine or other irritant reagents. On the whole, however, we are comparatively powerless against such parasites. And the same may be said with regard to the brood of young worms whose wanderings in the body, after boring through the wall of the intestine, we have hardly any means of preventing. Against these prophylaxis is our only security, and on this we may here lay the greatest emphasis, and claim for it more attention than it has yet received.

But before we can comply with the conditions of the prophylactic method, we must, above all things, know the ways and means by which parasites and their germs are introduced. We must, in other words, study the life-history of the several parasites, for this alone can put us in possession of the desired information. In this connection helminthology has still a mighty task before it, for as yet there are but few human Entozoa whose history and fate are perfectly determined. We do not wish to conceal the difficulty of the problem; it will yet be long before we can boast of a perfect solution. But the end is

well worth striving for, since it means nothing else than the health and weal of many thousands. This is no exaggeration; we have already noted the devastation which the *Dochmius intestinalis* makes among the Fellahs of Egypt, and we know of similar occurrences in other places. According to the report of Schleissner and Thorstensen, a seventh part of the population of Iceland suffer from *Echinococcus*,[1] and in tropical countries of the old and new world diseases caused by worms are among the most frequent and widely distributed, *e.g.*, tapeworm, dracontiasis, hæmaturia, chlorosis, and dysentery.

ETIOLOGY.

Our positive results as to the transference of human worm parasites are still unfortunately very far from complete; we must therefore content ourselves to a large extent with suggestions and deductive conclusions. The following remarks, therefore, make no pretension to exhaust the subject, but they nevertheless contain almost all that we are as yet warranted in maintaining.

We may first summarise in a sentence the chief result of our previous study of parasitic worms, viz., that the great majority of these creatures inhabit different animals in their different stages. If we apply this sentence to those infesting man, we see at once the probability of the conclusion, that *we derive a large proportion, and in all likelihood by far the largest proportion, of our parasites from other animals.*[2] Specially, then, must those animals be considered with which we come into contact in any way, and, above all, those domestic animals which are used as food.

[1] *Echinococcus* is widely distributed in Asia and Australia, and is, according to Schleissner, the most frequent of all diseases in Iceland. In 2600 cases of illness mentioned in the medical reports, 328 were afflicted with *Echinococcus* in the liver; and out of 327 private patients, 57. According to Krabbe, these results are not accurate, and by no means applicable to every district of Iceland.—(*Archiv f. Naturgesch.*, Jahrg. xxxi., Bd. i., p. 114, 1865.) According to a calculation of Finsen's for the northern part of the island, Krabbe would conclude that only $\frac{1}{40}$ or $\frac{1}{50}$ of the population can be proved to be suffering from *Echinococcus*. But even this is a very large number.

[2] A complete statistical account of the human Entozoa even of civilised Europe is still a desideratum. An effort has recently been made in this direction, on the basis of clinical dissections,—K. Müller, "Statistik menschl. Entozoen:" Erlangen, 1872,—based on the results of the autopsies in Erlangen and Dresden; and H. Gribbohm, "Zur Statistik der menschlichen Entozoen:" Kiel, 1877. From these results we learn that among us *Trichocephalus*, *Oxyuris*, and *Ascaris* are by far the most common Helminths. In Erlangen there were found, among 1755 bodies, 227 with *Ascaris* (12·9 p. c.), 213 with *Oxyuris* (12·13 p. c.), 195 with *Trichocephalus* (11·11 p. c.). Among these 138 *post mortem* examinations of insane patients from the asylum are not included, in whom round-worms were always found, sometimes only one species, sometimes several. In Dresden (out of 1939 *post mortem* sections) the numbers were much smaller,—*Ascaris* in 9·1 p. c., *Oxyuris* in 2·1

The correctness of this conclusion is indubitably established by experience and by experiment. Other animals furnish us, then, with the largest contingent of our parasitic guests, but they transmit them in very different stages. The parasites which we derive from the animals used in food are adult forms, like the common tape-worm and *Trichina*. We receive them, however, in a larval state, the tape-worm in the form of the bladder-worm, the *Trichina* in its encapsuled form among the muscles. Both these common forms are most commonly derived from the pig, while *Tænia saginata* is derived from the ox. On the other hand, our household animals mostly furnish us with the eggs or embryos of their parasites, which then attain in us their larval stage. Among the latter class of animals the dog is pre-eminent as the chief bearer of parasites. From him we derive *Pentastomum denticulatum*, *Cysticercus tenuicollis*,[1] and especially *Echinococcus*, which arise when the ripe eggs of his *Pentastomum tænioides*, *Tænia marginata*, and *Tænia echinococcus* respectively are in some way or other smuggled into us.

The manner of infection varies according to circumstances, and is largely determined by chance. It would be useless toil to recount all the conceivable possibilities, but a few must be noted. The eggs of

p. c., *Trichocephalus* in 2·5 p. c. Gribbohm reports for Kiel (out of 1117 examinations), *Ascaris* in 18·3 p. c., *Oxyuris* in 23·3 p. c., and *Trichocephalus* in 32·2 p. c.; and estimates the sum total of sufferers from parasites in all to be 43·5 p. c.; and after deducting children under half-year, at 49·8 (in women, 53·8 p. c., in children half a year to 15 years old 50 p. c., in men 46·7 p. c.). The other parasites have only a small percentage in comparison to the round-worms. Out of 1117 cases *Pentastomum denticulatum* was found in 12; *Cysticercus cellulosæ* 6 times; *Echinococcus*, 3 times; *Tænia saginata*, twice; *Tænia solium* and *Trichina* each once. I add further that among the 3694 *post mortem* sections reported by Müller there occurred 17 cases of *Tænia solium*; 5 of *T. saginata*; 36 of *Cysticercus cellulosæ*, 9 of *Echinococcus*. (In Göttingen, Förster found, among 639 bodies, 3 with *Echinococcus*, and 4 with *Cysticercus*.) According to Daconta (*Zeitschrift für Epidemiologie*, Th. i.) there is one tape-worm patient in Thüringen for every 3315 inhabitants; in the medical districts of Eisenach, Apolda, Jena, and Weimar, however, there is one for every 486. For the town of Hanover even 2 p. c. of tape-worm patients have been computed. Cruse found in Dorpat *Bothriocephalus latus*, at 482 *post mortem* dissections, in 6 p. c. (*Dorpater med. Zeitung*, Bd. ii., p. 315), *Ascaris lumbricoides* in 9·9 p. c. In comparison with these statements, I remark that Krabbe saw in Copenhagen and the surrounding district, among 500 dogs, 336, that is 67 p. c., infected with Helminths. *Ascaris marginata* was found in 24 p. c.; *Tænia marginata* in 14 p. c.; *T. cucumerina* in 48 p. c. The rest of the Helminths occurred much less often—*Tænia cœnurus* in 1 p. c.; *T. serrata* in 0·2 p. c.; *T. echinococcus* in 0·4 p. c.; *Bothriocephalus* sp. in 0·2 p. c.; *Dochmius trigonocephalus* in 2 p. c. ("Recherches helminthologiques," p. 3: Copenhagen, 1866). It was different in Iceland, where Krabbe found, in 100 dogs, *Tænia marginata* 75 times; *T. cœnurus* 18 times; *T. echinococcus* 28 times; the *T. cucumerina* 57 times; *T. lagopodis* 21 times; *Bothriocephalus* 5 times; and *Ascaris marginata* only twice. There were only 7 dogs free from parasites in Iceland.—*Ibid.*, p. 21.

[1] Krabbe considers the occurrence of *Cysticercus tenuicollis* in man as doubtful, *Ugeskrift fur Laeger*, Bd. xxxvii., No. 5, 1862.

Pentastomum tænioides, reaching the exterior in the nasal mucus, are transferred to us usually when the dog caresses us or licks our hands. They may also find access directly to our food, such as bread and salad, or may be deposited on vessels which we use in eating and drinking. In the same way, and especially by dirty dishes or food, are the eggs and embryos of the dog's tape-worm imported into us, and this is all the easier since the eggs are not voided singly from their host, but enclosed by the joints, which not only have a power of spontaneous motion, but may, in virtue of the glutinous surfaee of their body, be carried about in many ways. The eggs of these animals also frequently reach us through the medium of water used for drinking or washing purposes.

One must not, however, think that the existenee of a parasitie larval stage necessarily presupposes an importation from another animal. It sometimes happens that man infects himself. This is indeed eonstant in the case of *Trichina,* the embryos of which are, as we know, born free in the intestinal canal of their host, whence they wander without further change into the muscles, there to become the well-known encapsuled worms. Man may also infect himself with embryos of *Tænia solium,* if he transfer the ripe joints or the eggs alone into his stomach. I think it impossible, however, that any such self-infection could take place directly in the intestine. This has already been affirmed by Küchenmeister, but the liberation of the embryo presupposes a removal of the egg-capsule, and, so far as we know, this never occurs before the eggs have passed through the stomach. Experiment further contradicts Küchenmeister's supposition. In two cases where I succeeded in introducing eggs of *Tænia serrata* into the intestine of a young rabbit, by means of a fine syringe introduced through an opening in the abdominal wall, the animal remained free from bladder-worms.[1] If Küchenmeister's view were correct, then every one who suffers from tape-worm ought also to suffer from bladder-worm, which, as is well known, is not the case. But if, as often happens, we do find bladder-worms in those who suffer or have suffered from tape-worm, that is because, when a tape-worm is present, the introduction of joints or eggs is obviously an easier matter than when they have to be brought from another man, not to speak of other obvious possibilities, of which I mention merely these —that a patient harbouring a tape-worm may in vomiting easily run a risk of transferring some part, or it may be only a few joints, of the worm into his stomach; and further, that in sleep, when the joints,

[1] This experiment, through which Küchenmeister still ("Parasiten," 2d ed., p. 115, note) looks for the final decision of this question, has been long made by me, indeed fifteen years ago!

as not unfrequently happens, issue forth individually and creep about on the body, it may happen that, simply by a wipe of the hand or some other means, they are unconsciously transferred through the mouth to the stomach.

Encapsuled *Trichinæ* and bladder-worms are not, however, by any means the only Entozoa which man derives from himself. The supposition of Küchenmeister, that the *Echinococcus* also belonged to the number of the "Autochthones" has, however, proved erroneous, for the sufficient reason that the tape-worm, of which it is the immature stage, does not occur in man.[1] On the other hand, we have in *Oxyuris vermicularis*[2] a parasite whose transmission very commonly takes place by self-infection. The eggs which under favourable circumstances—*e.g.*, a temperature 37·5° C.—produce in a few hours a mature embryo, and which are found strewed about in the neighbourhood of the infested individual, and often in quantities even on his body, are transferred in various ways, but usually by the hands, to the intestine, and there the embryos escape and rapidly attain sexual maturity. This extreme liability to self-infection, and the continual reproduction of the parasites, are the causes of the persistency of *Oxyuris*-disease and of the difficulty of a perfect cure, which is indeed so great that it suggested the possibility of there being eggs which developed directly in the intestine of the host to sexually mature forms.

Trichocephalus dispar resembles *Oxyuris.* Davaine believes, however—what is not firmly established—that the eggs even of *Ascaris lumbricoides* may, with enclosed embryos, be accidentally introduced into man. The transference is, however, not so direct as in the case of *Oxyuris,* for between the laying of the eggs and their transference a period of many months usually elapses, during which the eggs have, of course, most diverse fortunes. Nor is it necessary that the eggs be derived from man, for both these worms are found in the pig, though they are then not unfrequently classed as distinct species (*Trichocephalus crenatus* and *Ascaris suillæ*).

From these results, we see that we cannot possibly regard our domestic animals as solely responsible for the introduction of the eggs of parasitic worms. We are ourselves partly to blame; we infect our own bodies, and sometimes also those of our fellow-men, just

[1] The opposite opinion rests on a confusion of *Tænia nana*, v. Sieb., which is a human parasite, with *T. echinococcus*, v. Sieb. (*T. nana*, van Beneden). The way in which Küchenmeister uses this confusion ("Parasiten," 2d ed., p. 163, note) as a reproach against me is so strange that I cannot refrain from asking the reader to peruse my harmless remarks, which have given that author occasion to raise his voice against zoologists (see p. 341 of the first German edition).

[2] See Vol. II.

as do animals with which we are associated. The foregoing remarks have had reference specially to the Entozoa, but these are far from being the only parasites which we derive from our association with other men and animals. It is in fact still more true of the Epizoa, whose transference takes place exclusively in this way. Lice, fleas, mites, find their way to us only through more or less direct contact with other organisms, and may be transferred in all forms, not only as eggs, but also, and that more commonly, in their adult state.

It is in the highest degree improbable that Entozoa are ever transmitted as adult organisms. Küchenmeister has indeed maintained this in regard to *Oxyuris*, and affirms that it may pass from a man

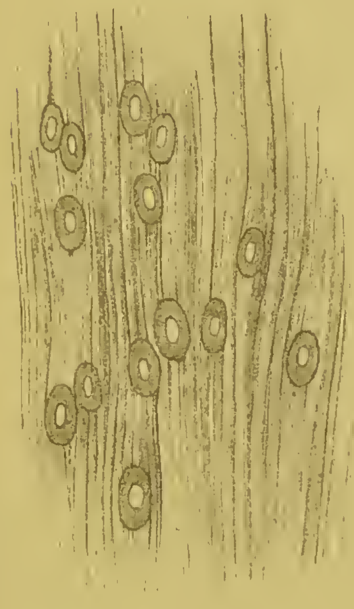


FIG. 91.—Flesh of pig with bladder-worms (nat. size).

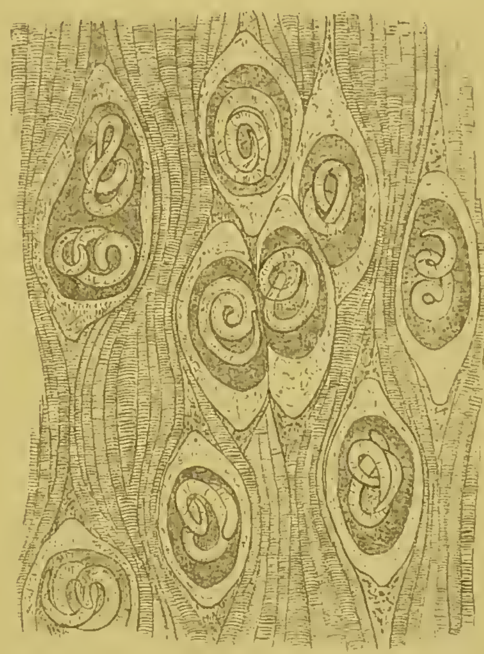


FIG. 92.—Flesh of pig with *Trichinæ*. (× 45.)

to his bedfellow. The supposition has at first sight much probability, for these worms at certain periods, and especially in the evening, issue spontaneously from the anus, and wander round about. I have even seen a patient in whose case the *Oxyuris* had during a night-sweat ascended as high as the shoulder.[1] But since the transference could only take place *per anum*, that presupposes circumstances

[1] Michelson describes a case (*Berliner klin. Wochenschrift*, No. 33, 1877) in which the *Oxyurides* had occupied the diseased groin of a boy for a dwelling and breeding place. Compare also the observations previously cited (p. 144) as to the occurrence of Nematodes on diseased skin.

which only exceptionally occur. Further, our deeper insight into the life and developmental history of *Oxyuris* has rendered Küchenmeister's supposition, which was never directly proved, somewhat obsolete and gratuitous.

Although the number of the parasites which we thus derive by external contact from man and beast is by no means a small one, yet it is very considerably exceeded by that contingent which we acquire along with our food and drink. The ox, whose flesh we eat, harbours, as we know, a whole host of young worms (Figs. 91 and 92), which only become mature in the human intestine. From the pig we derive *Trichina* and *Tænia solium*, from the ox *Tænia saginata*, just as the cat gets its tape-worm (*Tænia crassicollis*) from the mouse, and the mouse its *Spiroptera* from the meal-worm (*Tenebrio molitor*). In regard, then, to the helminthological relations of animals, this is the first and most general law, as we have already remarked (p. 80), that the carnivorous animal derives a great part of its Entozoa from its food. But besides the animals actually eaten as food, those also contribute their Entozoa which are accidentally swallowed or carried in some way into the alimentary canal. This mode of introduction (p. 80) obtains among the Herbivora; and of course it is not man only, with his almost equally vegetarian and carnivorous diet, that is subject to these parasites, but even the Carnivora, which avoid vegetable food, are not safe from their accidental importation.

We shall discuss in the first place *the transmission of parasites by the use of flesh as food.*

When flesh is eaten raw, as is the custom in Abyssinia and elsewhere, the possibility of transference requires no special proof. The worms thus swallowed develop as surely and constantly as in animals under experiment, provided only that they find in their new host the conditions essential for their further development, and that they are not injured by the mechanical processes of eating. It is thus sufficiently evident why *Tænia saginata* is found in young and old among the Abyssinians who eat raw beef, and why Europeans are also rapidly infested when they begin to live *à l'Abyssinienne.*

It is obviously otherwise among civilised peoples, where it is customary to cook the flesh used as food. The danger of infection with the young worms is by this means to some extent lessened, though the protection thereby afforded is only a limited one.

We may first of all note that, in spite of the general prevalence of the custom of cooking food, there are yet bye-ways open for the introduction of parasites. Raw meat is prescribed by the physician in many diseases as a specially nutritious food. During the preparation of certain kinds of food (especially sausages and meat-balls) the raw

flesh is tasted by the butcher, cook, or housewife, in order to estimate the proper quantity of salt and pepper. Further, in this state it forms the favourite food of many persons, and even whole classes—*e.g.*, the workmen in the manufacturing districts of North Germany. It may also happen that we derive parasites from sausage or ham which has come into contact with infected pieces of flesh or with living worms in the butcher's shop. The bladder-worm of the pig, or its 'head,' is often accidentally introduced in this fashion, especially since the butchers, knowing the law against measly flesh, take the greatest care always to cut away and remove the parasites when they appear on the surface. Where the custom of private slaughtering prevails, as in the middle-class families of North Germany, the parasites may be found in the kitchen or store-room, and thus arise many possibilities of transference and importation. One may, of course, urge that a bladder-worm could hardly be overlooked, or inadvertently swallowed, but the 'head' is enough for the development of the tape-worm, and being easily separable, could not in this state be distinguished from a little lump of fat without close examination.

Cooking—even boiling and roasting—is not a constant or sufficient protection against infection. It has indeed been asserted and observed that living intestinal worms (usually *Ligula*,[1] but sometimes also the so-called *Filaria piscium*[2]) are occasionally found in boiled or baked fish. Experiments were made by Pallas[3] and by Bloch,[4] in order to test the truth of this. The worms were cooked—some alone and some within their hosts, which are usually small. The results were, however, only doubtful, but it is impossible any longer to doubt the correctness of the statement. By my experiments in 1860, published in the first edition of this work, I proved that trichinous flesh is by no means thoroughly disinfected by the usual treatment, and as little by salting as by smoking. This statement, which therefore applies to salt pork, smoked sausage, and ham alike, has been corroborated both by observation and experiment,[5] and thoroughly overthrows any faith in the

[1] See a case cited by Rosenstein ("Kinderkrankheiten," 3d ed., p. 445, 1774) of such a worm found living in a cooked bream.

[2] Such a case was related to me by my since deceased friend Dr. Krüger, in Brunswick. A tolerably large cod-fish, which was cooked and brought to table, contained in its flesh many dozen living *Filariæ*.

[3] *Neue nord. Beiträge*, Bd. i., p. 98, 1781.

[4] "Abhandl. von der Erzeugung der Eingew. Würmer," p. 3 : Berlin, 1782.

[5] Compare Küchenmeister, Haubner, and Leisering, *Bericht über das Veterinärwesen Sachsens*, p. 188, 1862 ; Rupprecht, "Die Trichinenkrankheit," p. 112, 1864 ; Fürstenberg, *Wochenblatt der Annalen der Landwirthschaft*, No. 30, p. 274, 1864 ; Kühn, *Mittheilungen des landw. Institutes*, p. 1-84, Halle, 1865 ; Perroncito, "Sulla tenacita di vita del Cisticerco," *Annali Accad. Agricoltur di Torino*, vol. xix., 1876, and vol. xx., 1877.

harmlessness of the flesh we use as food. One must not of course think that heat and smoke (pyroligneous acid) and salt are without any effect on the parasites lurking in the flesh. On the contrary, one is at once convinced that these various influences are wholly, though to different degrees, hurtful to the worms; but this also is certain, that the action must attain a certain intensity and last a certain time before the worms die. *Trichina* does not perish till acted on by a temperature of from 62° to 69° C., but the temperature which usually prevails in the interior of the flesh during boiling or roasting is often somewhat below this, and in the case of large masses or rapid cooking, is so very far from it that the interior remains bloody. In such cases neither the developmental power nor the life of the inmate could be very seriously affected. Much the same may be said of other (cold) methods of smoking; we know of many and serious illnesses which have resulted from the parasites derived from ham or brain-sausage. The danger of partaking of such kinds of food is greater, since *Trichina* sometimes remains living for months in masses of flesh so preserved.

I may further take this opportunity of noting that *Trichina* has a special and uncommon power of resisting external influences. It can not only remain living for weeks in the summer time in putrefying muscle, but is, to a most remarkable extent, insensitive to cold or frost. During the coldest part of January (at about — 20° to — 25° C.) I left a portion of trichinous flesh for three days and three nights in the open air, and after thawing it in cold water, gave it to a rabbit. I hardly looked for any result, and was most astonished, after an interval of three weeks, to find the animal emaciated and paralysed. Death ensued eight days later, and I then convinced myself that it was throughout infested with *Trichinæ*.

Such considerations make it probable that the facts established in the case of *Trichinæ* cannot be directly applied to other worms. Indeed, Cysticerci are killed by a temperature of 50° C.,[1] and therefore much sooner than the *Trichinæ*. Their possible length of life in preserved foods is also shorter, rarely exceeding four or five weeks. But there is here also sufficient possibility of infection, which is indeed easy enough in the case of *Tænia saginata*, since beef is often eaten in a half-raw state, even after cooking.

To allay the apprehensions of our reader, we must not forget to mention that infection through the medium of boiled or roasted flesh is on the whole rare, since in the great majority of cases the parasites are killed by the ordinary culinary treatment. This is as true of *Trichina* as of

[1] This is the result of Perroncito's experiments, which agree with some which I have lately made. Lewis fixed the necessary temperature at 62·5 C., Pellizari even at 67·5 C.

bladder-worms, as statistical results clearly prove. Thus, according to official reports, there are above 30,000 swine eaten yearly in Leipsic, out of which, according to the results of the Brunswick investigations (which furnish as yet the most favourable fraction—one trichinous pig in 5000), there ought to be at least six infested with *Trichina*. If the parasites were not rendered harmless by cooking, we ought obviously to expect six epidemics of *Trichina* yearly, while in reality, apart from a few isolated cases, there have been only two observed since 1860—a severe one in the winter of 1877, and another less serious. In Sweden, where in many districts 1 per cent. of the swine are trichinous, the disease is only known as a sporadic malady, and as such only rarely.[1]

We have spoken mainly of the pig and the ox, since these animals furnish the largest proportion of the food used by civilised peoples, and, so far as we know, are the most common sources of parasites. But we are also aware that other kinds of flesh may also infect us with parasites. Thus the goat harbours the cystic stage of *Tænia saginata*, though not so frequently as the ox; the sheep and deer sometimes contain the bladder-worms of *Tænia solium*. Further, we may find *Trichina* in the flesh of martens, foxes, rats, and hamsters which are here and there used as food. The assertion of Herbst, that pigeons and other birds were also infested with encapsuled *Trichina*, is based on an error, for we are not yet acquainted with any bird capable of infecting man with worms. It is otherwise with fishes, for we have obtained convincing proofs through the observations and experiments of Braun,[2] in Dorpat, that the pike (although it remains questionable whether this is the only fish that does so) yields young stages of *Bothriocephalus latus* to human beings. It is to be assumed that *Bothriocephalus cordatus* of Greenland is also derived from the flesh of some marine fish which harbours its young stage. It is found not only in man but in dogs, which are fed by the Esquimaux, for the most part, on raw or dried fish. At any rate, it must be some inhabitant of the water which harbours the young stage of the human *Bothriocephalus*, as we infer with every certainty from the ciliated coating, by means of which the embryos are able to swim about.[3]

The introduction of the germs of Helminths can also easily take place through small terrestrial or aquatic invertebrates. Chance

[1] See Vol. II.

[2] Braun, "Zur Entwicklungsgeschichte des breiten Bandwurmes:" Würzburg, 1883.

[3] The assertion of Knoch (*Virchow's Archiv f. pathol. Anat.*, Bd. xxiv., p. 243 *et seq.*, 1862) that *Bothriocephalus* is developed without an intermediate host, was suspicious in the highest degree, even before Braun adduced arguments against it.—(See under "Bothriocephalidæ,"

must, of course, determine many of the methods of infection. We should as little think of eating a living snail as a bladder-worm. But such an animal is easily hidden among salad and vegetables, which we eat raw; and this is specially likely when they have grown in damp places, as is the case with water-cresses. Similarly, when eating roots, fallen fruit, &c., we may easily swallow worms, insects, and other small animals, without noticing it, and be infected with parasitic germs of various kinds; and where such creatures are eaten as food or as tit-bits, as happens especially among savage peoples, other methods of infection are obviously open.

We know, of course, as yet but few instances which prove a transmission accomplished in this way. Infection with *Tænia cucumerina* must be referred to this class. This parasite occurs not unfrequently in children, and is transmitted through the dog-louse (*Trichodectes*), in which the worm passes its immature stages;[1] but this mode of transmission is probably rare and local.

Under some circumstances, drinking water is the medium of infection. This is especially the case when the water is derived from ponds or reservoirs inhabited by numerous small organisms, or abounding in organic remains. Small Crustacea (*Cyclops*) swallowed along with the water transmit the Guinea-worm, which, according to Fedschenko,[2] passes its early life in these animals. And besides transmitters of parasites, we find here and there in such water free-living immature stages of such worms as *Dochmius trigonocephalus*, which are carried with the water into the intestine, and there settle down.[3]

The older physicians were wont to emphasise the use of fruit and raw vegetables as the means of introducing certain forms of worms, and this is, in a certain sense, as we now know, perfectly justifiable; but only in a certain sense, for we know with absolute certainty of no instance, either among men or animals, where vegetable food furnishes in itself either a transmitter of parasites or a parasitic germ; yet the possi-

postea.) The same may be said of the old conjecture, that the common custom of watering celery beds, &c. with the liquid contents of dung-heaps resulted in the importation of the eggs of *Bothriocephalus*, which at once developed into tape-worms in the intestine, especially as the eggs of Helminths found in dung-heaps can hardly ever be in a condition capable of germination. Otherwise, it might be supposed that infection with bladder-worms (not, as is sometimes said, with tape-worms) was sometimes brought about in this way by the eggs of *Tænia solium*.

[1] See Vol. I., also Melnikoff, *Archiv f. Naturgesch.*, Jahrg. xxxv., Bd. i., p. 62, 1869.

[2] See Vol. II.

[3] See Vol. II. I may add that Perona and Grassi ("Sullo sviluppo dell' Anchylostoma duodenale," Pavia, 1878) have meanwhile proved, by their researches into the immature state of *Dochmius duodenalis* what Wucherer also (*Gazeta medica di Bahia*, No. 65, 1869) had previously shown, viz., that the life-history of *Dochmius trigonocephalus* was similar to that of this worm.

bility of such being the case must in nowise be overlooked.[1] We are, of course, dealing only with the ordinary course of events, for vegetables are as liable as flesh to an accidental association with either adult or embryonic parasites. We have, indeed, every reason to suppose that along with raw vegetable food certain thread-worms (especially *Trichocephalus* and *Oxyuris*) very commonly find their way into man in the form of eggs, containing embryos.

It seems very doubtful whether there be any internal worms which bore their way into man, like the itch-mite or female chigoe. The only example which could be cited of such a mode of infection was the Guinea-worm, and in regard to this form also the theory has been disproved by the above-mentioned observations of Fedschenko.

The itch-mites and chigoes behave like those parasitic insect-larvæ which occur in superficial organs, like the larvæ of *Œstrus* in the sub-epidermal connective tissue, or the larvæ of *Musca* found in the ear passages, or in the nasal cavity, &c. The latter differ, indeed, in this—that it is the free-living mother which places them in these various situations.[2] When the grubs are found living in the intestine, the introduction of eggs or larvæ has taken place mostly by means of cold meat, cheese, &c., just as we saw to be the case with the intestinal worms; or in some instances the eggs may have come directly from the mother, having been laid on the lips or tongue during sleep.

Cases of parasites actively forcing an entrance into man are then rare and restricted to a few forms. The true parasites—the parasites κατ᾽ ἐξοχήν—exhibit no instance of it, and thus we may conclude that *the accidental introduction of eggs and immature stages is, after all, by far the most frequent and most constant source of the human Entozoa.*

Every one exposed to one or other of these modes of introduction, runs the risk of being infected with worms of various kinds, according to circumstances.

OCCURRENCE AND DISTRIBUTION.

One often hears of a certain liability to helminthiasis varying with age, sex, and even nationality.

[1] The statement of Ercolani, that the *Anguillula* and *Rhabditis* of plants become genuine parasites after their transference into the intestine of animals, rests upon a delusion. [On the other hand, the fact that the introduction of *Distomum hepaticum* is effected from water-plants or marsh-plants, on which its Cercariæ are encapsuled, has been made extremely probable through the investigations of Thomas and myself.—R. L.]

[2] As a rule, these insects are only induced to lay their eggs by some evil-smelling excretion. On this point see v. Frantzius, *Virchow's Archiv f. pathol. Anat.*, Bd. xliii., p. 98, 1868.

I have, indeed, expressly stated (p. 85) that certain individual characteristics, such as age, exercise a distinct influence on the development of the imported germ; but at the same time I believe that the majority of cases cited in support of the theory of a definite liability, will admit of another interpretation. When, for example, we find that children are more frequently infested by thread-worms, or by *Tænia cucumerina*, than adults, and that they are but rarely subject to the common tape-worm, that does not denote, in my opinion, that children[1] have a greater disposition to the first-mentioned worms, but only that they have, in the natural conditions of their life, much more opportunity to infect themselves with the larval stages of these parasites. I need only urge in support of my contention that children eat or suck all sorts of things without choice or distinction, and have therefore abundant opportunity to infect themselves with various transmitters of parasites, with which they would not, under ordinary circumstances, come into contact.

In the same way we may explain the very abundant occurrence of parasites which Vix has lately shown to be attendant on those mental diseases which are characterised by voracity. The "dirt-eating," which Vix would regard as a consequence of the helminthiasis, seems more probably the cause of it.

Nor is it, of course, a sign of a special "predisposition" that the female sex suffers more frequently (in the proportion of two to one according to Wawruch) from *Tænia saginata* and *T. solium*, since the household duties of women expose them to a much greater danger of infection by cystic worms. If not, we must consistently credit cooks and butchers with a similar disposition to tape-worm, and even to sporadic trichinosis, since they are of all persons most troubled by these parasites.[2] It is the trade which explains the frequency, just

[1] According to Gribbohm (*loc cit.*, p. 7), the per-centage of children below ten suffering from *Ascaris* is 24·6, as compared with an average of 18·3. Similarly, as regards *Oxyuris*, the per-centage is 31·6, as opposed to the average 23·3; and in the case of *Trichocephalus*, 33·3, as compared with 32·2. The total number of children below twenty infested with intestinal Nematodes is not less than 62 per cent., while the average for all ages is only 43·5. The number of the cases used as a basis of calculation—(Gribbohm bases his conclusions on 1117 *post mortem* examinations)—is, of course, much too small to give certain results. In this way, we can understand how Müller, depending on the statistical results of the Dresden and Erlangen Hospital ("Zur Statistik der menschlichen Entozoen," Erlangen Dissert., 1874), contradicts the commonly received opinion, by stating that *Ascaris* and *Oxyuris* are not, on the whole, more frequent among children than among older persons. We may further note that *Tænia cucumerina* has only been observed in children and never in adults.

[2] This observation dates from the beginning of this century, and seems to have been first made by Fontassin. Wawruch, to whom we owe the most extensive information as to the statistics of the tape-worm, found that of 206 patients more than a quarter belonged to the above occupations.

as it is abstinence and not nationality which protects the Europeans in Abyssinia from tape-worm (p. 156).

In judging such cases, we must, above all, remember that *the frequency of the occurrence of intestinal worms is determined primarily by the opportunities for the transmission of the embryos or larval forms.* Customs, habits, occupation, and mode of life deserve the first consideration, and have a much greater influence on the occurrence and distribution of parasites than age, sex, or nationality can ever have. After what we have said, it may indeed appear as if the etiological import of the latter factors were after all only apparent, or at least dependent on the numerous inter-relations between them and the true causes.

What we have emphasised above explains why *the appearance of certain forms of helminthiasis is often in striking dependence on conditions of time and space.*

In the first connection we have as yet but little material as far as man is concerned, and what we have is uncertain, in so far as many parasites have a somewhat long life, and do not at once attract attention. We may, however, advance thus much,—the thread-worm is said to be most common in autumn,[1] as we might indeed expect from its rapid growth already mentioned, whilst *Tænia solium*, on the other hand, according to the results of professional helminthologists, calls for treatment more frequently in summer, which leads us to regard the infection as having taken place in winter, since the tape-worm requires several months before it makes itself noticeable by the expulsion of proglottides. Indeed, one can hardly doubt that it is in the winter months that the increased consumption of flesh, and the custom of killing animals used for food at home, afford specially favourable opportunities for infection with bladder-worms. For similar reasons *Trichina*, with only a brief period of incubation, is far more frequently observed in winter than in summer.

The evidence furnished by the worm diseases of our domestic animals is still more convincing. These occur in most obvious dependence on certain periodically recurrent causes. The sheep-cough (*Strongylus filaria*), which attacks our flocks in late autumn, may with certainty be said to arise from the meadow pastures, just like the Cœnurus, which appears mostly at Christmas, or like *Echinorhynchus gigas*, which only appears in those swine which have been fed in the open air. Even our geese are infested with worms (especially with *Tænia lanceolata*) only while they are seeking their food through

[1] According to Gribbohm, the maximum of cases of *Ascaris* occurs in February (*loc. cit.*, p. 9). In the same way, *Oxyuris* is most prevalent in January, and *Trichocephalus* in April. There are fewest cases in August, October, and November.

field and pasture, and afterwards lose them during the subsequent fattening.[1]

It is also a well-known fact that liver-rot (*Distomum hepaticum*) and verminous inflammation of the lungs (*Strongylus*) are much commoner among our horned cattle in some years than others. We even know of epidemics of this kind which have in many districts almost destroyed the cattle for a long time. Wet seasons especially have this pernicious result, since long-continued rainy weather assists the transportation of the young brood or of the intermediate host, and greatly increases the possibility of infection.

Even among human parasites there is one, on the occurrence of which a damp season has an undeniable influence. This is the *Filaria Medinensis* of the tropics, the periodically varying degree of whose occurrence has long excited the attention of observers. The register of the native general hospital in Bombay shows, according to Carter,[2] that during the years 1851 and 1858 the maximum of sixty-three cases occurred in August, the minimum of twelve in February, and forty-four in the month of May. The results of observations in a military hospital ought to be still more reliable, since the soldiers would at once seek relief on the discovery of the trouble. And these results are so far different, that—*e.g.*, in Sattara, a garrison town 100 miles from Bombay—three-fourths of all the cases were treated between March and June. According to the observations of seven years, the maximum occurs in May (125 cases) and in June (102), and the minimum in January (11). We may therefore conclude that it is in the two months at the end of the dry season and beginning of the wet that the disease most frequently manifests itself. From many cases of infected sailors who have spent only a short time in a place it has been determined that the Guinea-worm requires ten or twelve months for its perfect development, and we can therefore further conclude that it is during the rainy season that this parasite finds entrance.[3]

The local and endemic occurrence of parasites must be discussed from the same point of view. We should expect, *a priori*, that the frequency of helminthiasis would be in inverse ratio to culture and civilisation. Filthy and careless habits, the frequent eating of raw

[1] Bloch has already recognised this fact ("Abhandl. über die Erzeugung der Eingew. Würmer," p. 10, 1782), and has correctly found its reason in the altered nourishment. In other cases the parasites acquired in youth, during a particular time, continue on into later life. Thus, for instance, the *Polystomum* of the bladder and the *Opalina* of the rectum in frogs, both date from the time of the larval condition. See Zeller, *Zeitschr. f. wiss. Zool.*, Bd. xxvii., p. 238, 1876, and Bd. xxix., p. 352, 1877.

[2] *Ann. and Mag. Nat. Hist.*, ser. 3, vol. iv., p. 110, 1859.

[3] For further details see Vol. II.

food, and especially of raw flesh, insects, and snails, the close association of man and beast, and, in short, all the external characteristics of savage life, are, as we have seen, most important causes of parasitic diseases, and facts, so far as we know them, bear this out. Nowhere are intestinal worms more frequent than among savage peoples, especially in the tropics, as has been long ago sufficiently established, and lately confirmed by travellers and physicians, especially in the case of Africa. In Abyssinia, for example, every inhabitant, male or female, is infested with intestinal worms from his fourth or fifth year. Similar results might be given in regard to the American slaves, the Esquimaux, and the Burätis, among the lower class population of the East Indies. Of course the same parasites do not prevail throughout. The negroes of the West Indies are specially plagued with *Ascaris;* the Abyssinians most commonly harbour *Tænia,* due, as has been supposed since the time of Bruce, to their general use of raw meat. Since the flesh of swine is avoided by the Abyssinians, it is of course not *Tænia solium,* but *Tænia saginata,* which occurs. The latter is associated with the ox almost throughout the world, while the former, like *Trichina,* is specially prevalent in those lands where swine are generally bred.[1] A difference may even be observed in neighbouring districts like North and South Germany. In Berlin *Tænia solium,* and accordingly its related *Cysticercus cellulosæ,* are not at all rare in man, but both so uncommon in Vienna that physicians sought long in vain for the latter, and not being in a position to distinguish *Tænia saginata* from *Tænia solium,* regarded the reports of the Berlin physicians as to the frequent occurrence of bladder-worms in the eye with unconcealed distrust. We can similarly understand how the famous helminthologist Bremser, living in Vienna, was never convinced of the existence of a circle of hooklets in the human tape-worm till Rudolphi sent him the head of a *Tænia solium* from Berlin. Where the use of flesh decreases, the supply of certain Helminths becomes less copious, the worms themselves being less numerous; but the difference may

[1] In Denmark Krabbe found *Tænia solium* only 53 times in 100 cases of tape-worms, *T. saginata* 37 times, *T. cucumerina* once, and *Bothriocephalus* 9 times. The proportions were similar in Giessen, where out of 57 tape-worm patients only 12 were infected with *Tænia saginata.* On the other hand, among 35 tape-worms observed in Florence by Marchi, there was only a single *Tænia solium.* But these proportions vary according to circumstances. Thus Krabbe writes to me that since 1869, up to which time the above numbers held true, *T. saginata* has become relatively more frequent in Copenhagen and its surroundings. Out of 78 new cases since that time, there were only 16 of *Tænia solium,* but not less than 46 of *T. saginata,* 4 of *T. cucumerina,* 10 of *Bothriocephalus.* Krabbe looked for the cause of this partly in the *Trichina*-panic, which had considerably restricted the use of raw swine's flesh, partly in the greatly increased use of raw beef in illnesses. And in Northern Germany, according to my personal experience, the occurrence of *Tænia solium* has in a decennium become much less frequent.

be annulled by greater negligence in the preparation of the food. This is especially true of trichinosis, which is hardly less frequent in the villages and among the lower classes than it is in towns and among the well-to-do, although the number of tape-worms, especially when compared with that of thread-worms, is considerably less in the former than in the latter.

It is impossible, without special knowledge of the various life-histories, to bring the local conditions of parasites into relation with the customs and manner of life of the inhabitants. We must, therefore, leave many of these problems as yet undetermined, *e.g.*, where the 63 per cent. (according to Bilharz and Meckel) of Fellahs and Copts derive the *Distomum hæmatobium* from which they suffer, or why *Filaria sanguinis* is so frequent in tropical countries.

On the other hand, we can at once understand the similar distribution of *Dochmius duodenalis* when we remember that this worm passes its youth freely in water, and that stagnant or slowly flowing water is oftener used for drinking in tropical than in colder zones. Similarly we are probably justified in referring the frequency of *Echinococcus* among the Icelanders, and other pastoral peoples, to their close and constant contact with numerous dogs,[1] and to the generally associated want of cleanliness. This disease seems to have been in former centuries much more frequent in Germany than it is now, when custom demands that dogs be kept at a greater distance, and when the dog-tax has also very considerably lessened the number of those animals.[2]

We have spoken as yet only of the local occurrence of helminthiasis, without special regard to its geographical distribution. The latter is, in many respects, independent of custom and mode of life. It is determined, on the whole, less by man than by the distribution of the intermediate hosts, and by the temperature of the region.

The importance of warmth as a factor in the distribution of worms may be inferred from what we have already seen (p. 73), that a certain temperature is requisite for the development of the embryo. When this temperature is not attained, or does not last long enough to be efficient, the worm cannot continue to exist. Thus, *Ascaris lumbricoides* is wanting in those tracts where the temperature does not

[1] On this point consult Krabbe ("Recherches helminthol.," p. 60), who also mentions that in Iceland there is one dog for every eleven inhabitants, while in Germany there is only one for every fifty, and that besides *Tænia echinococcus* is much commoner in Icelandic than in German dogs (see p. 152, note).

[2] When (1883) the dog-tax in the Grand Duchy of Baden was lowered from 3 florins to 1-1½ fl. yearly, the number of dogs increased to one for every twenty-eight inhabitants, while before, with at a tax of 3 fl., and now with a 4 fl., there was only one to every forty-nine.

rise above 20° C., or only attains it for a short time. It is all but unknown in Iceland (according to Krabbe), although distributed throughout the Temperate and Torrid Zones. *Trichocephalus* has a more restricted distribution, since its eggs require still greater warmth. If the temperature required for hatching were in itself decisive, *Oxyuris* (with a requisite temperature of 38° C.) ought hardly to be found outside the tropical countries, while in fact it is extraordinarily abundant in the far north, and more widely distributed there than elsewhere (Ohlrick). This cosmopolitan distribution is explained when we consider that the above-mentioned high temperature is only needed for a few hours to develop the embryos. The warm skin of man affords the requisite conditions of development equally well among the Esquimaux as among the natives of tropical climes. The *Oxyuris* patient thus bears the means of infection on his own person—transmission to the mouth is a simple matter—the easier, the less the attention paid to the cleanliness of the body and clothing.[1]

We hardly need to discuss how the distribution of Helminths is affected by the habits of the intermediate hosts. Where they are absent there can obviously be no parasite.[2] Parasite and intermediate host are in their occurrence as closely bound up with one another, as Herbivora and the plants upon which they feed.

We cannot doubt that in the course of time, when our knowledge of the life-history of human intestinal worms is more complete, we shall be able by the discovery of the intermediate hosts to explain the causes of the more or less restricted distribution of some of these parasites. It is especially in regard to the as yet but little known tropical Entozoa that we look for further progress in this direction. The only tropical worm whose intermediate host we know is *Filaria Medinensis,* which passes its larval life in animals (*Cyclops*) which are among the most frequent inhabitants of our fresh water. This seems hardly to justify the hope expressed above, but we must remember that, besides the factors emphasised above, many chances of the most diverse kind influence the occurrence of parasites.

It not unfrequently happens that even when the conditions of occurrence are present, the species occur in one place abundantly, but are entirely absent even in the near neighbour-

[1] It is therefore not so surprising that *Oxyuris* occasionally occurs in sucklings. Gribbohm saw them in infants five weeks old, but *Ascaris* and *Trichocephalus* only in the eleventh month (*loc. cit.*, p. 6). In contradiction to this statement, however, we read in Göze: "We find instances of large thread-worms voided by infants hardly a month old, who have tasted only their mother's or nurse's milk" (*loc. cit.*, p. 66).

[2] Thus, *e.g.*, *Tænia serrata*, so common in Germany, is not found in Iceland, where there are no hares or rabbits (Krabbe).

hood.[1] Just as for free-living animals, so for parasites, there are within the area of distribution certain more or less restricted haunts, in which the creatures occur either exclusively or at least much more frequently. Where any intestinal worm has once established itself in virtue of a fortunate combination of favourable conditions, there it remains for long, indeed till the conditions change, for the possibilities of infection increase in proportion to the number of the parasites.[2] In this way there arise what have been called "foci of infection," especially in our time in the case of *Trichina*, but also of tape-worms and other parasites. By such "foci," helminthiasis may be spread over an ever-increasing area. Thus *Filaria Medinensis* has been carried by slaves from the west coast of Africa to Tropical America, and has thus obtained a wide distribution. Since the intermediate host of this parasite is one of our commonest animals, the worm is therefore in no way restricted to Asia or warmer climates, and its acclimatisation in our own country is by no means an impossibility.

When opportunities of infection multiply in any way, then there arise, even among men, decided worm-epidemics. Knox tells of a formidable tape-worm epidemic which broke out in October 1819 among the English soldiers engaged in the Kaffir war, after they had been feeding for a lengthy period on the flesh of overdriven and unhealthy oxen.[3] Similarly, in the year 1820, a fourth part of the Egyptian army serving under Mohamed Bey in Kordofan suddenly fell victims to Guinea-worms after they had remained healthy for two years.[4] And according to Bartholin and Küchenmeister the "fiery serpents" of the Old Testament were most probably Guinea-worms.

The epidemics of *Trichina* which occur every year in North Germany are so well known that it seems almost unnecessary to devote special attention to them. An epidemic appearance of *Ascaris* has also been described in former times. But what they then called worm-epidemics were mostly dysenteric troubles, in the course

[1] [For an instance of this in the case of *Distomum*, see Thomas, *Quart. Journ. Micr. Sci.*, N. S., vol. xxiii., p. 99, 1883.—W. E. H.]

[2] In the Punjaub, where *Tænia saginata* is in certain sections of the population almost as frequent as in Abyssinia, in 1869, according to official reports, not fewer than 5·55 p.c. (in 1868 even 6·12 p.c.) of the oxen slaughtered at the military stations were infected, and badly so, with cystic worms.—(See *Lancet*, p. 860, Dec. 1872.) The natural occurrence of Cysticercus in cattle is exceedingly rare with us. Similarly *T. marginata*, *T. cœnurus*, and *T. echinococcus* in dogs, are in Iceland 4, 18, and 47 times commoner than in Denmark (Krabbe), and the same proportion holds for the related cystic stages.

[3] *Froriep's Notizen*, Bd. i., p. 122, 1822. Friedberger observed a disease due to tape-worms among pheasants, *Zeitschr. f. Veterinärwiss.*, p. 97, 1877.

[4] Clot, "Aperçu sur le ver dragonneau," Marseilles, p. 30, 1830.

of which thread-worms were often seen to be voided. It is, however, doubtful whether these worms were directly concerned in the disease, though it is in no way improbable that thread-worms should under abnormal circumstances be introduced in extraordinary numbers.[1]

The foregoing discussion has shown us the ways and means by which man becomes infested with intestinal worms or with their larvæ. It may also serve to anticipate a rational prophylaxis, or to suggest the lines along which this must be sought. The first law of this prophylaxis is simply, *shield yourself from every circumstance by which parasites could be introduced;* but the difficulty of following this out in detail is as great as the law is short; we cannot protect ourselves against unknown and unseen foes such as we have here to deal with. Helminthiasis will never disappear; nevertheless a rational prophylaxis can limit its propagation and restrict its distribution, and in so doing confer a great benefit on health and life.

This prophylaxis depends above all things on cleanliness, especially in the kitchen and house. Raw foods cannot be too carefully inspected, whether they be of vegetable or animal nature. Flesh must be kept away from the preparation of other food (bread) and from the dishes and other vessels used. Cooking ought to be characterised by due carefulness; sausage and ham bought in small quantities from the butcher ought to be subjected to close scrutiny. Still more should flesh which is eaten raw be carefully examined. Water, and especially drinking water, should be clear and pure. Dogs and other domestic animals should be kept out of the kitchen and dining-room. Contact with them should be as far as possible restricted, and should be at once wholly suspended when they in any way show suspicious symptoms of helminthiasis. The food of dogs and pigs should consist preferably of cooked stuffs, and never (as in slaughter-houses and skinning sheds) of the remains of slaughtered or of dead animals. Rats, which infect the pigs with *Trichina*, ought to be kept away from the styes. Excrement should be deposited in inaccessible places, and any tape-worms present (especially *Tænia solium*) removed as speedily as possible.

Precautions such as these should be taken against the worms prevalent in Europe. Other rules apply to the Epizoa, and especially concern contact with other men, *e.g.*, in the use of beds, linen, and clothes.

All this is in the first place applicable only to individuals and families. When similar dangers threaten to affect the community,

[1] Göze mentions ("Versuch. einer Naturgesch., u. s. w.," p. 23, note 2) the case of a family in Brunswick, in which all the members, from father to child, and even the two maids (two workmen alone excepted), were infected with *Ascaris*.

more thorough-going measures must be taken in regard to water-supply, dung-hills, and drains, as well as in regard to slaughter-houses and the treatment of the flesh. What has already been provided for by sanitary regulations is by no means sufficient nor in keeping with the progress of science. We shall refer only to the regulations about measly flesh, which in many places allow it to be sold raw, if the bladder-worms are "not numerous," though never in the form of sausage or similar preparations, though it is just this last process which renders the cystic worms somewhat harmless. The measures taken against *Trichina* also admit of manifold improvement. It is above all necessary to popularise the facts known about parasites and their origin, and even to make this a subject of instruction in schools.

SECTION II.

SYSTEMATIC ACCOUNT

OF THE

PARASITES INFESTING MAN.

INTRODUCTION.

The number of parasites as yet observed in man, including some doubtful species and merely temporary visitors, amounts to nearly sixty. We know no other creature which harbours so large a number, but it is open to question whether this may not be simply due to the fact that special attention has been devoted to man and human parasites. On the other hand, we can hardly suppose that the whole list of human parasites is yet known to us. From the results of the last few years, we are led to the conclusion that there is still, especially beyond the bounds of Europe, a crowd of unknown human parasites. Nor is our knowledge of European species yet exhaustive; we know of many doubtful forms, and have been enabled in our own day to render the catalogue more complete.

Of course the parasites infesting man have not by any means equal importance from a medical point of view. Besides dangerous or even fatal forms, we find others which usually exert hardly any influence whatever on the health of their host. The study of their distribution reveals also similar differences. Some—though on the whole only a few—are exclusively restricted to man;[1] others infest other animals also, and many of these occur indeed more frequently in other than human hosts, which they may perhaps have visited only once by chance; and further, we know that some of our parasitic visitors (larvæ of insects) generally prefer free life to parasitism.

Most parasites infest the human body only in their adult and sexually mature state; but to this statement also there are exceptions. Some species, such as *Tænia solium* and *Trichina spiralis*, are found in man in two stages, while others are only parasitic in their larval or intermediate form, *e.g.*, *Tænia echinococcus*, as a cystic worm.

As regards the special parts of the organism which are infested, we find that in man the skin and the intestine are, as usual, most exposed to the assaults of parasites. By far the greater number of parasitic species concentrate themselves in these two organs, and only a fourth of the whole number are found throughout the rest of the body. Yet there is hardly any part of the body which is without

[1] With the increasing completeness of our knowledge of helminthology, the number of these parasites is becoming ever smaller. Thus I have lately found in the gorilla, not only *Ascaris lumbricoides*, but also *Dochmius duodenalis*, which had previously only been found in man.

its parasitic guest, which may be either a definite and peculiar form, or one which occasionally visits other organs, and which may perhaps only occasionally wander from them. Of this we shall, in the course of our systematic study, find abundant illustration, and it is at this stage only necessary to observe that the distribution of parasites within the human body is very diverse and unequal. While some species are confined to definite, and perhaps strictly limited areas, others wander to the most various organs, and some (*e.g.*, *Echinococcus*) hardly seem to avoid any part of the body.

As regards their systematic position, the parasites of man belong to three different divisions of the animal kingdom—the Protozoa, the Vermes, and the Arthropoda. The Vermes furnish the largest contingent, the Protozoa the smallest—but both only internal parasites—while the parasitic Arthropoda are almost wholly external.

SUB-KINGDOM I.—PROTOZOA.

THE organisms which, following von Siebold, we here include under the name "Protozoa," form a division of the animal kingdom whose members, in part at least, can only be distinguished with difficulty, if indeed at all, from the lowest plants.[1]

The most essential characteristic of these Protozoa lies in their minuteness and in the simplicity of their structure, two characters which to a certain extent involve each other. For the most part invisible to the naked eye, and but rarely attaining the diameter of a millimetre or more, they possess a body devoid of anything deserving the name of organs, and often discharge their vital functions as simple minute masses of animal substance, without any differentiation whatever.

As early as 1845 von Siebold endeavoured to compare the structure of the Protozoa with that of the ordinary cell, or, in other words, to define the Protozoa as unicellular animals;[2] and this assumption has been fully justified in regard to the vast majority of these organisms. It is, however, true that we have in the course of time discovered some Protozoa in which as yet a nucleus has been sought for in vain (the so-called "Monera"), and others which might perhaps be more correctly termed cell-aggregates, as evidenced by the possession of numerous nuclei, were it not that in all these cases the component cells are so

[1] It is not my intention to enter further into the relations between plants and animals. This much, however, must be noted, that in the simplest animal and vegetable organisms we find neither in structure nor in function any of those fundamental differences which usually separate the higher representatives of the two kingdoms. From this it does not, however, in any way follow that we are bound to separate off these simple organisms from the others, and make a special intermediate kingdom of them, as Hogg and Haeckel have lately done (Protoctista, Hogg—Protista, Haeckel). By the creation of this heterogeneous intermediate kingdom, which includes forms so widely separated as the Infusoria and Fungi, the difficulty of determining the boundaries is not diminished, but doubled; instead of there being only one uncertain boundary line, there are two. [With respect to this point, it may be urged that a scientific classification is not merely an arrangement for practical convenience, but rather a method of expressing our views as to the relations of organisms. If, in conformity with the evolution theory, we hold that plants and animals sprang from a common stem, then "Protista" must have once existed, and if so, they ought to find a place in our scheme. The question whether it is easier to draw one boundary line or two seems quite beside the mark.—W. E. H.]

[2] "Lehrbuch d. vergl. Anat. d. wirbellosen Thiere:" Leipzig, 1845; and *Zeitschr. f. wiss. Zool.*, Bd. i., p. 270.

slightly separated that the structure of the whole organism is hardly perceptibly modified. While in other animals tissues arise fitted according to their properties for the discharge of various functions, the Protozoa possess only a body-substance more or less homogeneous in nature and similar in functional capacity.

Since we have learnt to recognise in the cells of an organism not only the ultimate anatomical elements, but also the physiological units of all vital processes, and are, in other words, convinced that the single cell lives and represents an organism (elementary organism, according to Brücke), it cannot any longer seem strange that there are plants and animals which consist only of a single cell, or at least of something equivalent, and which nevertheless perform essentially the same vital processes as higher organisms, built up, perhaps, of millions of cells.

An animal of this kind possesses neither muscles nor nerves, and has yet the capacity of motion and of sensation; it receives and digests food without an alimentary canal, secretes without glands, and reproduces its kind without sexual organs. All the functions which in the higher organisms are severally discharged by diverse and definite groups of cells and cell-derivatives, are here perfectly discharged by a single cell, which constitutes the body of the animal.

This body is not, however, always of perfectly homogeneous character; for in spite of their general simplicity, the Protozoa often exhibit a certain histological and physiological differentiation similar to that which we observe in the individual cells of higher organisms.

Not only is the outer surface of the living protoplasm often hardened to form a cuticle, which permits of ingestion and excretion only endosmatically, but the protoplasm itself exhibits a differentiation into a firmer outer portion, more or less exclusively the seat of motion (and sensation), and a more fluid inner portion, which discharges the functions of digestion and absorption. Like the protoplasmic contents of the muscle cells, the contractile outer sheath can even acquire a fibrillar consistency, by which it becomes fitted for even more energetic discharge of its functions; and through the contractility of the outer portion, vacuoles, which originate there, become established as pulsating vesicles. Here and there, too, in the body-substance, holes and openings appear, which, breaking through the cuticle and ectosarc, represent the mouth and anus, much in the same way as similar arrangements occur in the cells of higher animals (*e.g.*, the so-called "goblet-cells") for like purposes. In many cases (among the Infusoria) further differences may be based even on the varied form and fate of the nucleus.

Thus we see that even among the Protozoa numerous and striking

modifications of structure are beginning to appear. In many cases this differentiation induces a sort of superficial resemblance to more highly specialised organisms, such as worms and other multicellular creatures, which, in opposition to the Protozoa, have been lately called "Metazoa." We can thus understand how it was that a famous investigator once attempted to interpret the organization of the Infusoria (which are, however, conspicuously Protozoa) entirely in accordance with the analogy of higher, and indeed of the highest animals.[1]

This attempt, indeed, was made at a time when there was not only no knowledge of the structure of the single cell, nor true insight into the histology of the animal body, but when the Infusoria were almost the only Protozoa known. Through the discovery and study of other forms (especially through the labours of Stein, Johannes Müller, Lieberkühn, Haeckel, and Hertwig), a belief in a "perfect organization" of the Protozoa has become impossible, for the vast majority of them are destitute of that differentiation which distinguishes the Infusoria, and exhibit characters which stamp them indisputably as unicellular organisms.

If we are rightly to express the morphological nature of the Protozoa, we cannot of course support the old idea of Schwann, according to which the cell was "a hollow nucleated vesicle, surrounded by a transparent structureless wall," in which the contents are of only subordinate importance. While it is true that the cell membrane is, in virtue of its properties of firmness, porosity, &c., of most fundamental physiological importance in the economy of the cell, yet, on the other hand, it is equally certain—thanks especially to the investigations and generalisations of Max Schultze—that it is by no means the essential part of the cell. It is indeed not to the surrounding membrane, but to the living protoplasm—to the formerly undervalued cell-contents—that the characteristic capacities of the cell are to be referred. Movement and irritability, assimilation and growth—in a word, all the vital phenomena of the organism—are dependent on the properties of this protoplasm.

We cannot retain the slightest doubt on this point when we remember that there are cells, both among higher and lower organisms, which never become enclosed in a membrane at all, or only at a late stage, but which in their naked membraneless state exhibit the phenomena of life even more conspicuously than the normal membrane-clad cells.

In these naked cells one can observe, under certain circumstances, and especially in their normal conditions, a peculiar movement. The protoplasm gathers itself at certain convenient points in the form of processes, which grow out under the eye of the observer into lobular or

[1] Ehrenberg, "Die Infusionsthierchen als vollkommne Organismen:" Leipzig, 1838.

finger-like prolongations, which sometimes branch, and, after a time, are again drawn in. With this change of form there has also been a change of position, the cell creeps along by means of its processes, moving slowly, but in a definite direction. Solid particles are thus enclosed by the soft protoplasmic mass, and, if their nature admit of it, may be dissolved or altered. We can even feed the cells in the same manner as Infusoria with particles of pigment, and watch these as they remain for a while within the body substance.

It is not difficult to understand the lively interest which these phenomena excited when first closely observed in the white blood-corpuscles of vertebrates.[1] And this was naturally intensified when men became convinced that they had here to do not with a unique peculiarity of these corpuscles, but with a fundamental property of animal protoplasm. Of course some cells may exhibit this phenomenon in a particularly conspicuous and lively fashion. Thus, only to mention one or two examples, the blood-cells of lower animals (*e.g.*, of *Thetis*, Fig. 93), according to Haeckel, may be much more easily fed, and exhibit more conspicuous movement, than those of vertebrates, which, for the purposes of observation, require the aid of a warm stage

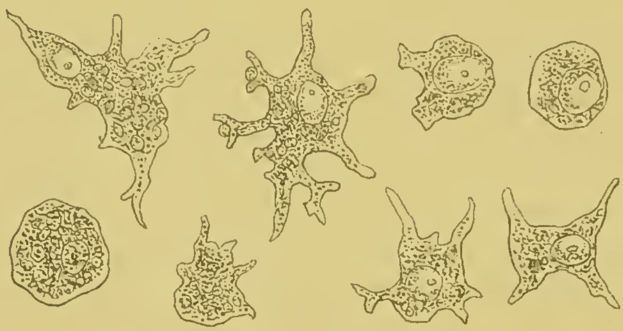


Fig. 93.—Blood-corpuscles of *Thetis*, partly with enclosed granules of pigment (after Haeckel).

or similar appliance. Again, the membraneless eggs of sponges and polyps exhibit amœboid movements in a most wonderful way. The same is true of segmentation spheres, which often show beautiful "migrating cells," which not unfrequently devour and digest the granules of the yoke, just like independent organisms.[2]

This comparison is all the more necessary since there are numer-

[1] Max Schultze, *Archiv f. mikrosk. Anat.*, Th. i., p. 1 *et seq.*, 1862. Among previous observations I may specially mention those of Lieberkühn.—*Müller's Archiv f. Anat. u. Physiol.*, p. 14, 1854.

[2] See Reichenbach, "Die Embryonalage und erste Entwicklung des Flusskrebses," *Zeitschr. f. wiss. Zool.*, Bd. xxix., p. 153, 1877 [and also Metschnikoff, *Quart. Journ. Micr. Sci.*, vol. xxxiv., p. 89, 1884.—W. E. H.].

ous forms among the Protozoa which are hardly distinguishable from these naked cells, except by their free life. Of such animals the best known are the *Amœbæ* (*Proteus diffluens* of the old zoologists), which are often found in crowds in the sediment of fresh and salt water (we shall speak later of an *Amœba* parasite in man), and which in structure and function correspond so closely with the naked cells, that we are accustomed to call the latter "amœboid" cells, or to describe their movement and method of nutrition by this term.

Nor are these *Amœbæ* distinguishable from cells in the nature of their reproduction. In both this takes place by division, from the nucleus outwards, through the surrounding protoplasm, and results in the formation of two distinct masses out of the originally simple body-substance. A strictly sexual reproduction has not yet been observed with certainty in any of the Protozoa.

It is further to be noted that the *Amœbæ* are by no means the only Protozoa which are, in structure and function, interchangeable with the cellular elements of the higher animals. The other groups also contain similar forms in greater or less number.

This resemblance is not without importance in the history of our science. Even in our day certain parasitic Protozoa (which, as we shall afterwards see, are very numerous) have, on the ground of this resemblance, been often considered as component parts of their host, and inversely some cells, in reality belonging to the host, have been classed as parasites. As illustrative of this latter case I need only refer to the so-called "Spermatozoa," which, as is well known, were quite generally ranked as parasitic animals till the time of Kölliker, and were on the strength of this idea frequently credited (even by Ehrenberg, Valentin, and others) with more or less perfect internal organs. So deeply rooted was the notion of the animal nature of these bodies, that it still prevailed even when the existence of living spermatozoa had been long recognised as indispensable to semen capable of fecundation. The only concession in consequence of this fact was to regard the spermatozoa as "necessary parasites." At that time, too, observers further deceived themselves with the thought that the blood corpuscles might be other similar "necessary parasites" (Mayer).

It is a still more difficult task, as already hinted, to determine the boundary between parasitic Protozoa and some similar parasites of vegetable origin. With regard to the latter, I have principally the Schizomycetes in view, organisms which, on account of their motile powers, were very generally referred to the animal kingdom as *Bacteria* and *Vibriones*, although their nearest relations, the Phycochromaceæ (*Oscillatoria*, &c.), containing chlorophyll-granules, are decidedly plants. In former times it was the fashion to call everything an

animal which moved independently, while we, on the contrary, are now acquainted with numerous plants and plant-embryos possessed of the power of locomotion, and are indeed, on the strength of the facts we have mentioned above, inclined to believe that contractility is a general property of (living) organic matter.

Those *Bacteria*[1] which we have mentioned are extremely small rod-like, sometimes spiral, or spherical, bodies, which always abound in decaying organic matter, and multiply so rapidly by transverse division that, as Cohn has calculated, a single individual (150,000 millions of which make up a milligram) may in forty-eight hours produce a mass of half a kilogram, and with good feeding may in three days leave a progeny of 7½ million kilograms, at least if those conditions which the calculation postulates ever actually occur.

They are, however, not only attendant on processes of decomposition and decay, but are able to originate and keep up these and similar processes, acting, like the yeast plants, as oxidising and reducing ferments, taking in or giving out oxygen. Thus they play a most important *rôle*, some occasioning ordinary putrefaction (*Bacterium termo*), others the butyric (*Bacillus butyris*), and others again the lactic and acetic fermentations. The so-called "mother of vinegar" of the latter consists essentially of an organism resembling *Bacterium* (*Mycoderma aceti*).

To this fact, the Schizomycetes owe their high importance in pathology, for they are found not only more or less constantly and plentifully in the excretions and fæces of animals (diarrhœtic discharges, purulent matter, alkaline urine, encrustations on the teeth, &c.), but also in the juices and tissues of the body, which must therefore be correspondingly altered by them. Thus the splenic fever of our domestic animals depends, as we now know with the greatest certainty, on the presence and growth of Bacteria (*Bacillus anthracis*) which infect the blood,[2] and which, on transference to man, may

[1] Of the voluminous literature on the subject of Bacteria I will only mention Cohn's researches, "Beiträge zur Biologie der Pflanzen," Hefte ii., iii., 1872 and 1873.

[2] Through the investigations of Koch and Cohn (*loc. cit.*), we now know the whole life-history of the usually motionless splenic fever *Bacteria*. As long as they are contained in the living host, they remain unchanged, but in the blood or suitable juices of the dead animal they grow out into a long unbranched thread, which develops numerous small shining spores. After these have been carried into a living body, they give rise to *Bacteria* again, which at once begin to divide. This transference may not take place for a long time, for the spores are able, without loss of their reproductive capabilities, to lie dried up for years, or to remain whole months in putrefying fluids, or even to endure alternately damp and dry environment. The transmission is probably effected by external contact, the spores being carried into wounds, perhaps along with dust. No infection is possible internally from the stomach. If the blood and tissues of the dead animal are rapidly dried, so that the *Bacillus* is unable to form spores, then the possibility of infection only lasts a few weeks.

give rise to malignant pustule: similarly pyæmia, small-pox, diphtheria, and other so-called "contagious diseases" are occasioned by *Bacteria* of extreme minuteness (*Micrococci*).[1] Even in recurrent fever the presence of a spirally twisted *Bacterium* (*Spirillum*) in the blood is a constant phenomenon. According to Koch, cholera is also caused by a *Bacillus* (*B. comma*).[2] Since our experience of the pathological nature of these structures is daily widening, we can understand how many modern pathologists would refer the infectiousness of all such diseases to the presence of active Schizomycetes. The old doctrine of "Contagium vivum" (p. 121) is thus resuscitated in a changed form.

If we inquire without prejudice into the reasons which lead us to refer the Schizomycetes to the vegetable kingdom, in spite of their animal-like nutrition and locomotion, we can give no other answer than this, that they belong to a phylogenetic series, which leads in uninterrupted succession to indisputable plants. The properties which they themselves possess hardly suggest a reason for separating them from the Protozoa, for the Schizomycetes are organisms of small size and simple structure, without cellular organs or tissues, and with exclusively (or at least predominantly) asexual reproduction. They are, in other words, creatures which in their organization do not (or at most only slightly) transcend the differentiation of a *simple* cell, and in fact are sometimes mere masses of protoplasm.

From the phylogenetic point of view, we can not only define the systematic position of the Schizomycetes, but are also enabled to restrict the Protozoa to the three classes of Rhizopoda, Gregarinida, and Infusoria. These also are, of course, not wholly without their points of contact with certain vegetable organisms, but are on the whole more closely linked to the animal kingdom, and in their highest representatives the Infusoria are certainly of the nature of animals.

The peculiarities of these three groups lie for the most part in their modes of nutrition and motion, but many other differences exist in their reproductive processes and general organization. The Rhizopoda, for example, with their naked mass of protoplasm, move by means of rapidly changing lobose or filiform processes (so-called "Pseudopodia"), which we have already seen in the *Amœba*, one of

[1] In regard to the organisms of the small-pox lymph, see Cohn, *Archiv f. pathol. Anat.*, Bd. lv., p. 229, 1872; and on those of diphtheria, see Oertel, *Deutsch. Archiv f. klin. Med.*, Bd. viii., p. 242, 1871; also Klebs, "Beiträge zur Kenntniss der pathogenen Schizomyceten:" Prag, 1874.

[2] [For an account of the controversy regarding the comma *Bacillus*, see Klein, "Micro-Organisms and Disease," Second Ed., London, 1885; also various papers in the *Lancet* and *British Medical Journal*, 1884 and 1885; and, for a brief summary of the question, *Nature*, vol. xxxi., p. 97, 1885, and Lankester, *ibid.*, p. 168.—W. E. H.]

the members of this group; the Infusoria, on the other hand, possess a permanent locomotor apparatus in the form of cilia; and the Gregarinida glide forwards in a more worm-like fashion by the contraction of their larger body-mass. Further, the Rhizopoda and Infusoria feed on solid, or at least somewhat firm food, which either (Rhizopoda) simply sinks into the protoplasm, or is ingested by means of a special mouth (Infusoria), while the Gregarinida are supplied with fluid food exclusively by endosmosis through the enveloping cuticle. The Gregarinida live wholly as parasites, and therefore in conditions which render the presence of either a temporary or permanent mouth unnecessary. It is equally intelligible that the mouth is, as we shall see, wanting even in some parasitic Infusoria (species of *Opalina*).

The term Gregarinida must, however, be restricted to those forms which are found usually in crowds in the alimentary canal or other viscera of some lower animals, especially insects and worms, and which have at the first glance a superficial resemblance to microscopic Nematodes, as which indeed they were formerly described. The name cannot be extended to allied organisms found parasitic on higher animals, for these differ in many ways from the true Gregarines, both in appearance and in life-history, though closely linked to them by the very characteristic reproduction by hard-shelled germs (the so-called "Pseudonavicellæ," or "Psorospermiæ"). I will therefore introduce the term "Sporozoa" to denote the forms above referred to.

All the three classes have, as the following survey will show, representatives parasitic in man.

Class I.—RHIZOPODA.

Protozoa, consisting of a membraneless mass of protoplasm, which forms lobose, finger-like, or filiform, and often branched pseudopodia, and taking in solid food without having a permanent mouth. Only a few forms are naked, the majority possess either a simple chitinous or a hard calcareous or siliceous skeleton, which is provided with more or less numerous openings for the protrusion of the pseudopodia, or may not unfrequently consist simply of single needles. Reproduction takes place partly by simple division, partly by actively moving germs produced within the body-substance.

In the simplest forms, the so-called "Monera," the body consists of an apparently non-nucleated mass of protoplasm, without further recognisable differentiation. At most, and that after rich feeding, the body is seen to be studded with small granules, which are only absent in the outermost portion. But as a rule, in the Rhizopoda, a distinct

nucleus can be further distinguished, which may either remain simple, or, with an increase of size, divide, and that often into a considerable number of nuclei. Again, a varying number of vacuoles may be observed, which sometimes exhibit a conspicuous and even rapid contraction. In the higher forms, the protoplasm becomes differentiated into an outer layer, and a central substance which encloses the nuclei, and may itself be enclosed by a porous membrane (Radiolaria). At the same time the body assumes a firmer consistency, and a stable, generally spherical, form, having, however, an appearance varying according to the degree of contraction, and generally showing a state of activity in the pseudopodia, which are protruded as lobose processes, almost as if flowing from the body mass. The form and nature of the pseudopodia vary generally according to the consistency of the protoplasm; their rigidity and fineness are usually proportional to the firmness of the body-substance. The movement of granules, which is often to be observed in most wonderful fashion on the thin Pseudopodia, is sufficient to prove that their substance, even when in apparent rest, is the seat of a continual molecular displacement.

We need say the less about the skeleton of the Rhizopoda, since that has only to be considered in the free-living forms, which only interest us here, in so far as they serve more fully to illustrate the general structure of the Rhizopoda. The Rhizopoda can evidently live only in a moist environment, indeed almost wholly in water, but are also found in the earth, and particularly in the thin moist moss or lichen-covered surface of trees and rocks. The skeleton of the fresh-water forms is usually of a simple membranous nature, forming a sort of shell, out of the opening of which the animals protrude their Pseudopodia. In the marine forms, the skeleton acquires a firmer character by taking in lime or flint, and is frequently of extraordinary beauty. This is specially true of the Radiolaria, which, with their needles and lattice work of flint, are among the most beautiful of microscopic objects. The calcareous skeletons are generally coarser and heavier, and lie quiescent with their occupants among foreign substances; while the Radiolaria, with their delicate skeleton and the radiating meshwork of protruded Pseudopodia, are often found floating in the water. Like the chitinous shell, the calcareous skeleton has often only a single opening, but in the majority of cases it is perforated by countless small pores through which the Pseudopodia issue (hence the name "Foraminifera"). The Polythalamia have a number of united chambers, which increase in number with the increasing size of the body. The closed form and immoveable walls of the house indeed necessitate a new building if the body is to increase in size.

These chambers in some species lose their continuity, and, retaining their contents, lead an isolated life; and this may be the more readily regarded as a form of asexual reproduction, since the single-chambered fresh-water Rhizopoda also not unfrequently protrude their contents to a greater or less extent out of the chamber, and by the secretion of a shell form a new organism.

Simple division (which, however, when the portions are of unequal size, looks more like budding) is apparently very common among the Rhizopoda. But we further find a second kind of reproduction, in which the body-mass, like the yolk of a fertilised ovum, falls into a varying number of pieces, each of which then becomes a distinct organism, and often finds its way to the exterior in the temporary form of a swarm-spore, provided with a single cilium. As an antecedent to this process, the naked so-called *Amœbæ* first surround themselves with a membranous covering, which encloses the body like a capsule; but this may be also secreted under other circumstances, *e.g.*, in the scarcity of water. Protected by this capsule, the creatures can undergo desiccation without danger, just as do the eggs of the Nematodes, previously mentioned (p. 53).

In those Foraminifera which have tests, the formation of the brood takes place in the several chambers, inside which the young are, in many species, surrounded by a shell, so that on the rupture of the enclosing test they issue forth resembling their parents.

The swarm-spores of Radiolarians arise in the central capsule—that is, in the nucleated central substance.

It was demonstrated as early as 1859, by Lambl, that the Rhizopoda included forms parasitic in man.[1] In the intestinal mucus of a child who died of enteritis, there were observed not only small naked amœboid organisms, 0·004 to 0·006 mm. in diameter, but also shell-bearing *Difflugiæ* and *Arcellæ* (0·01 to 0·016 mm.), which are found normally only in ponds and ditches. The representation which Lambl gives of these creatures is, however, so incomplete, that their identification seems in the highest degree suspicious. At any rate, such a discovery, so long as it remains uncorroborated, can hardly be regarded as established. But since we know from other quarters of the occurrence of a parasitic *Amœba* in man, it is a reasonable supposition that at least some of the observed bodies were indeed nothing else than parasitic Rhizopoda.[2] *Amœbæ* are also to be observed as parasitic in various conditions in other higher and lower animals;[3] but only

1 "Aus dem Franz-Joseph-Kinder-Spitale," Bd. i., p. 363, Taf. xviii.

2 Apart from the loose or otherwise altered epithelial cells, others might be referred to the group of Monads.

3 Thus, for example, Lieberkühn reports the occurrence of *Amœbæ* in the intestine of

the naked and not shell-bearing forms of Rhizopoda have been found. The latter we must, for other reasons, regard as exclusively confined to water or damp earth.

We must again, however, remember that fragments of cellular tissue may be easily confounded with true *Amœbæ*, and many so-called *Amœbæ* may be only a developmental stage of entirely different animals. We know even of active Rhizopod-like fungi (the so-called *Myxomycetes*), which, in their youth, are exactly like *Amœbæ*[1] (*Myxamœbæ*), and may, under certain circumstances, live for a long time as such.[2]

Amœba, Ehrenberg.

Auerbach, "Ueber die Einzelligkeit der Amœben," *Zeitschr. f. wiss. Zool.*, Bd. vii., p. 365, 1855.

Naked Rhizopoda, with a richly granular protoplasmic body-substance, surrounded by a thin hyaline layer, and enclosing, besides the nucleus, one or more contractile vesicles. The Pseudopodia are finger-like, sometimes lobose, processes, which become full of granules when they attain a certain size, and which vary in number and breadth according to the consistency of the body.

The form of the body may be generally described as spherical; but this undergoes during life a continual Protean change, as the animals flatten themselves out for movement, and then send out pseudopodia, now here, now there, indifferently. The size and structure of the latter differ sometimes very characteristically in the different species. When the protoplasm has only a comparatively slight consistency, the animals seem almost to flow along on their lower surface. The nature of the food varies according to circumstances, but in the free-living forms consists mainly of parts of plants. These are enclosed by the movements of the protoplasm, and are digested, the undigested residue being expelled by any part of the body indifferently. The only mode of reproduction as yet distinctly observed[3] is that of simple division, which is completed in a short time,

the frog (*Müller's Archiv f. Anat. u. Physiol.*, Bd. viii., p. 12, 1854). They are sometimes found in considerable numbers, and exhibit a somewhat rapid motion. Similarly, Waldenberg found amœboid animals in the intestinal canal of the rabbit, and once even inside an epithelial cell (*Archiv f. pathol. Anat.*, Bd. xl., p. 438, 1867). Amœboid parasites are also not unfrequently found in the intestinal canal of insects, such as beetles, &c.

[1] See the classic investigations of de Bary on Myxomycetes, *Zeitschr. f. wiss. Zool.*, Bd. x., p. 88, 1859 [and more recently Zopf, "Die Spaltpilze:" Breslau, 1883.—W. E. H.]

[2] According to Cienkowsky, *Archiv f. mikrosk. Anat.*, Bd. xii., p. 15, 1876.

[3] [More recently it has been demonstrated by the investigations of Maggi, Grassi, Brass, and others, that *Amœbæ* not only divide, but also, after encysting form swarm-spores, which resemble Monads both in appearance and in movement.—R. L.]

and, under favourable conditions of nutrition, rapidly repeated. Under some circumstances an encystation takes place, when the animal draws itself together into a sphere, and secretes a substance originally mucous in nature.

Amœba coli, Lösch.

Lösch, "Massenhafte Entwickelung von Amœben im Dickdarm," *Archiv f. pathol. Anat.*, Bd. lxv., p. 196, Taf. x., 1875.

The body measures from 0·02 *to* 0·035 *mm., is of a somewhat fluid and coarsely granular nature, and forms usually only one or a few blunt and broad processes. These arise suddenly, and are not unfrequently drawn in as suddenly, giving the otherwise roundish body a sometimes oval, sometimes pear-shaped, or even irregular form. In the interior, besides granules and food, a clear round nucleus may be recognised, as also several vacuoles, sometimes irregular in shape and of varying size.*

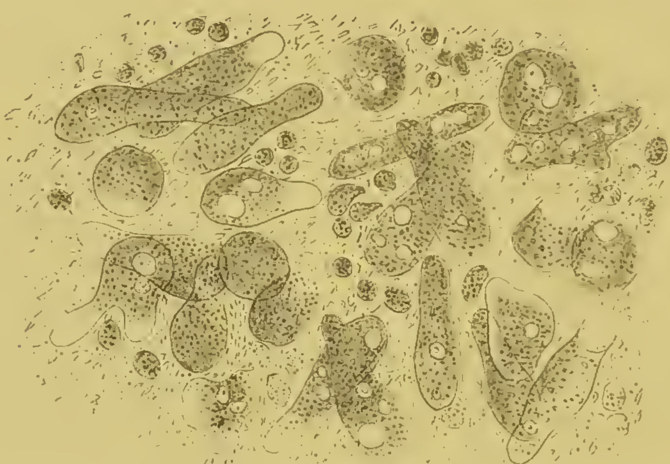


FIG. 94.—*Amœba coli* in intestinal mucus, with blood corpuscles, Schizomycetes, and similar bodies (after Lösch).

The *Amœba* thus shortly characterised (Fig. 94) has hitherto been only once observed, namely in St. Petersburg, in a peasant who suffered from an ulcerative inflammation of the large intestine.[1] It

[1] [Grassi states (*Gazetta med. Ital. Lomb.*, No. 45, 1879) that he has observed *Amœba coli* six times in Italy. The parasites were always present only in small numbers, and in persons whose health had undergone no change. Cunningham also, who not unfrequently observed the occurrence of *Amœba* in the human intestine, and still more often in the cow and the horse, is disposed to attribute to it no special pathogenic significance. The parasite occurs, however, in certain diseases of the intestine, especially in such as are characterised by alkaline excreta and in cholera, and its presence may then be referred to the specially favourable vital and developmental conditions found under such circumstances. Cunningham further holds that Flagellata parasitic in man are to be regarded

was abundantly found in the ill-smelling, thin, fluid stools, which also showed the usual contents of dysenteric stools—*i.e.*, besides remains of food—red and white blood corpuscles, detached intestinal epithelium, and cell fragments, and a great number of bacteria, micrococci, and monads. There was, however, no possibility of confounding the *Amœba* with other structures. In appearance, size, and mode of motion, they were sufficiently distinguished from the surrounding elements.

Although this case stands as yet alone, we can well believe that the occurrence of parasitic *Amœbæ* in similar intestinal diseases is both frequent and widely distributed. I am corroborated in this supposition, not only by the above-cited and questionable observation of Lambl, but also by an oral communication from my esteemed friend Dr. Sonsino, in Cairo, who found large numbers of an equally undeniable *Amœba* in the intestinal mucus of a child who had died of dysentery. Its size was from 8 to 10 times that of the blood corpuscles. Since the forms observed by Lösch were only 5 to 8 times as large as the red blood corpuscles, we may perhaps conclude that the Egyptian *Amœba* was of a different species. Steinberg also alleges the discovery of an *Amœba* (*A. buccalis*) in the mucus covering the teeth of man (*vide postea*).[1]

One can form some approximate conception of the immense number of *Amœbæ* living together in the intestine when one learns that Lösch often saw, with a magnifying power of 500, from sixty to seventy specimens in the same field of vision; and Fig. 94 (reproduced as closely as possible from nature) shows by no means the most thickly crowded portion.

The movements which first attracted the attention of the observer are described as follows:—"On any part of the surface of the body indifferently, a small, roundish, transparent, glassy projection appears, sharply divided from the rest of the granular protoplasm. This is either rapidly retracted, or, increasing quickly in size, it forms eventually a finger-like process, whose length approximates to the diameter of the rest of the body. This process is finally drawn in again, only to reappear at another point; or it may be that the granular protoplasm suddenly flows into it and fills it up. In this way the form of the whole animal changes, it becomes oval, elongated, or, where there are several processes, irregular. The processes are constantly blunt, never filiform, or running to a point.

as developmental stages in the life-history of a Myxomycete, which he calls *Protomyxomyces coprinarius* ("On the Development of certain Microscopic Organisms occurring in the Intestinal Canal," *Quart. Journ. Micr. Sci.*, vol. xxi., pp. 234-290, 1881).—R. L.]

[1] [Grassi speaks also (*loc. cit.*) of an *Amœba dentalis* observed by him in three cases. It is said to resemble *A. coli*, and, like this, to become quiescent at low temperatures (below 25° C.).—R. L.]

Their formation, as compared with the changes of a blood corpuscle, is characterised by great rapidity, for they are sometimes protruded and retracted four or five times in a minute. They arise, indeed, so suddenly as to produce the impression that the protoplasm flows out at a circumscribed portion, forming a little drop of mucus. The animals generally keep to one place during these movements, but sometimes they creep slowly about, first sending out a long transparent thread, then allowing the granular protoplasm to flow into this, and, lastly, drawing the rest of the body forwards. These changes of position take place comparatively slowly, the animals hardly advancing the length of their body in a minute."

The nucleus presents a globular, transparent, colourless, or faintly yellow appearance, and varies in diameter from 0·0048 to 0·0069 mm. It has but slight consistency, often changing its shape somewhat with the movements of the parasite, and becoming sometimes more oval or somewhat lengthened out, but regaining its original form on the withdrawal of the pressure. In quiescent specimens it lies more in the centre of the granular protoplasm, and is therefore observed only with difficulty; in actively moving forms it may occupy any position throughout the body, and often lies near the surface of the body. In the interior one may distinguish a nucleolus of very varied size and refractive power. In individual cases its diameter is half that of the nucleus. It is transparent, but in the smaller specimens shows a dark contour, and has such power of refracting light that it sometimes looks not unlike a fat granule. The vacuoles in the protoplasm are also of very varied size. Most of them are larger than the nucleus, but some are only half as large; exceptionally, one sometimes finds them half as big as the whole animal. Their number varies from one or two to six or eight, or even more, but the smaller numbers more frequently occur. In exceptional cases they seem to be wholly absent, and only appear after the addition of water. After prolonged observation, a distinct change of form is sometimes to be observed. They sometimes become rather smaller, sometimes larger, and, as the *Amœba* moves, may assume an oval or long bean-shaped, or even irregular form. Distinct pulsations cannot, however, be observed.

Besides the component parts, various foreign substances are sometimes found embedded in the protoplasm, especially *Bacteria, Vibriones, Micrococci,* and chains of *Mycothrix*; and exceptionally larger bodies, such as red and white blood corpuscles, nuclei of detached cells, starch grains, and other substances found in the intestine. After the application of an enema of vermilion, given to the patient to test the ingestive power of the *Amœbæ*, particles of the pigment were to be seen in their interior.

Unfortunately nothing is known of the life-history of *Amœba coli*. We do not even know its mode of reproduction. But the very abundant occurrence of the parasite leaves no doubt that reproduction, and that a most prolific one, does take place within the intestine. For in the hospital, where a continued supply of the parasite from an external source was hardly possible, no diminution was perceptible, though the daily voiding went on for four months. The most natural supposition is, of course, that the reproduction took place by division,[1] as has been directly observed in other *Amœbæ;* see especially F. E. Schultze's observations on *Amœba polypodia.*[2]

As regards the mode of transmission, we are of course left to hypotheses, which are all—numerous as they may be—without exception destitute of foundation, since we do not know whether the *Amœba coli* lives exclusively in the intestine, or is parasitic only accidentally. There are, indeed, some free-living species which closely approach this form in their appearance and mode of motion. Lösch has, in this connection, drawn attention to *Amœba princeps,* Auerb., but it seems to me to resemble still more closely *A. Jelaginia,* lately described by v. Mereschowsky.[3] This suggestion receives some probability from the fact that this form is found "in great abundance in the sand and mud at the bottom" of the Jelaginic ponds near St. Petersburg, in the same locality, that is, in which the above-mentioned patient had presumably become infected with his parasites.

The patient had lived a most miserable life, sleeping in half-built barracks, protected neither from wind nor rain, and was mainly occupied in dragging logs out of the water. It is, therefore, likely that he

[1] [In view of the above-mentioned formation of spores in *Amœba*, one can hardly help believing that this process plays an important part in the reproduction of parasitic forms, and this so much the less, since Grassi has published his investigations upon a species (*Amœba pigmentifera*) parasitic on *Sagitta* (*Rendiconto Instit. Lomb.*, vol. xiv., 1881); and since Brass ("Die thierischen Parasiten des Menschen," Cassel, 1884) and others have observed the same process in the intestinal *Amœbæ* of the mouse and frog.

Cunningham also observed an encapsulation in the case of his *Protomyxomyces*, when cultivated in the free state (in alkaline cows' dung). But within these cysts were developed, not swarm-spores, but resting-spores, with a cuticular envelope, which either remained in groups or separated from each other. From these spores Cunningham believes, though he has not actually observed it, that the ciliated intestinal parasites arise, which in their turn, after manifold variations, give rise to resting-spores again.—R. L.]

[2] *Archiv f. mikrosk. Anat.*, Bd. xi., p. 592, 1875.

[3] *Archiv f. mikrosk. Anat.*, Bd. xvi., p. 204, Taf. xi., Figs. 29 and 30, 1878. The description accompanying the figures runs as follows:—"The form of the body varies exceedingly. The body sends out short round processes, but the movements are not due to these, but to the *Amœba* flowing *en masse.* The contents consist of coarse and fine granules, both kinds being present in abundance. The ectoplasm is distinctly separated from the endoplasm. Besides the nucleus there are also some vacuoles visible, which contract very rapidly in the interior of the body. The consistence is fluid, the movement rapid. The diameter varies from 0·02 to 0·04 mm."

had often drunk impure and muddy water; but I am not at all inclined to identify his parasite with the above free-living form, for, in spite of much resemblance, there are also many differences (in size and behaviour of the vacuoles) between them.

The disease of the patient had, on the whole, the appearance of an intense and persistent dysentery, and on *post mortem* examination the large intestine was seen to be violently inflamed, and in some places, especially in the lower regions, ulcerated. To the important medical question whether the parasite stands in a direct causal relation to the disease or not, our author gives an unreserved affirmative answer. Lösch would at least insist that the *Amœbæ* aggravate the inflammation, and do not allow the ulcers to heal. He supports his opinion partly by referring to the immense number of the *Amœbæ*, which, by their uninterrupted movements, could not but cause a mechanical irritation of the diseased mucous membrane, partly by referring to the fact that during the whole course of the illness there was an undeniable relation between the number of the parasites and the intensity of the inflammation. Further, only the systematic use of quinine enemas,[1] which caused the parasites for a time almost wholly to disappear, had any effect in alleviating the malady. Pleurisy afterwards set in, followed by pneumonia, and death finally supervened, with all the phenomena of complete anæmia and exhaustion; and it was only in these last stages that the *Amœbæ* wholly disappeared, and the diarrhœa consequently ceased.

The convincing argument in favour of Lösch's opinion is the result of an experiment which he made. In order to get some direct evidence of the pathological import of these parasites he injected three dogs *per os et anum* with from one to two ounces of fresh stools containing these *Amœbæ*, and repeated the injection on three successive days. A fourth dog was similarly treated after an intense intestinal inflammation had been produced by enemas of croton oil. This was meant to show whether the *Amœbæ* were able to aggravate an inflammation already existing.

Only one of the experiments gave any positive results. One of the first three dogs, after recovering from the digestive disorder (vomiting and diarrhœa) which first appeared, seemed to be perfectly healthy; but eight days after the last injection a small mucous mass of about the size of a pea, and a bloody colour, was found in the otherwise normal excrement, and this on microscopic examination exhibited a great number of living *Amœbæ*. In the course of the next few days the number of *Amœbæ* thus voided rapidly increased,

[1] According to the experimental result of Binz, corroborated, indeed, by the above case, quinine is an efficient poison for organisms consisting of simple protoplasm.

though the general state of health remained the same, and showed no further abnormal phenomena. Since the elapse of two weeks resulted in no further change, and the excrement remained firm and normal in spite of the associated mucus, the dog was killed eighteen days after the first injection. On examination the mucous membrane of the rectum was found in some places reddened, irregularly swollen, covered with viscous blood-stained mucus, and superficially ulcerated in three places. The ulcers were roundish, of 4 to 7 mm. in size, and surrounded by swollen and exceedingly hyperæmic mucous membrane. Their base was irregular, and had a dark red appearance. The submucosa below was hyperæmic, swollen, moist, and turbid. The mucus in the rectum and in the ulcers was thickly crowded with *Amœbæ*, which differed in no respect from the injected parasites. The mucous membrane of the large intestine was normal, nor did the other organs exhibit any pathological character.

This experiment proves at least that these *Amœbæ*, if abundantly developed in the intestine, may give rise to violent irritation of the mucous membrane, and cause not only hyperæmia and increased formation of mucus, but also an intense inflammation, sometimes aggravated by ulceration.

Class II.—SPOROZOA.

[Davaine, "Leçons sur les Sporozoaires :" Paris, 1884.—R. L.]

Unicellular parasites of definite form, without pseudopodia or cilia, but covered by a smooth, more or less firm, cuticle. At the anterior end there is not unfrequently an organ of attachment, like a proboscis or cushion. Their movements are inconspicuous, worm-like, or slightly amœboid. They live wholly as parasites, and receive their food by endosmosis. Reproduction takes place by more or less hard-shelled spores (Pseudo-navicellæ, Psorospermiæ), which are formed in the interior of the adult, sometimes in very great numbers. Occasionally they appear gradually, but more often simultaneously, and then after the attainment of maturity and encapsulation. In these spores there develop, sooner or later, a varying but usually small number of sickle-shaped bodies, which, after creeping out, become new parasites. In other cases the contents of the spore are collected in a single amœboid embryo.

The most familiar examples of these Protozoa are the Gregarines (Fig. 95), which stand highest in their organisation and functional activity, and indeed represent a special group. They are, so far as we know, parasitic only in invertebrates, especially in insects and

worms, and usually occur associated in great numbers.[1] In certain animals, and especially in omnivorous species (*Tenebrio*, cockroach, earthworm, &c.), they are almost constant, so that one can hardly examine a specimen without finding Gregarines. They are harboured sometimes in the intestine, as in insects, sometimes in other organs, as in the testes of the earthworm, sometimes in the body-cavity.

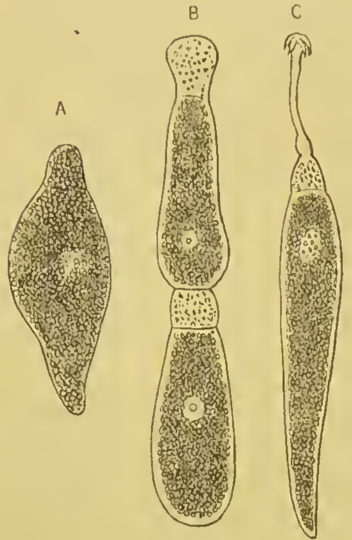


Fig. 95.—Gregarines. (*A*) *Monocystis agilis*, from the testes of the earthworm; (*B*) *Gregarina cuneata*, from the intestine of *Tenebrio*; (*C*) *Stylorhynchus oligacanthus*, from the intestine of a dragon-fly.

The body of the Gregarine[2] is more or less extended, and often saccular. The intestinal parasites are very constantly provided with a pad or proboscis like, sometimes even hooked, process, which serves as an organ of attachment, and if in the form of a sucker, may connect two animals together (Fig. 95, *B*). The protoplasm is more or less granular, according to the age and size of the parasite. It encloses a large vesicular nucleus with a nucleolus, and is surrounded by a porous cuticle, under which may be sometimes distinguished a thin, clear, sometimes striated, outer layer. The formation of spores takes place at the close of the individual development, when the animal has attained its full size, and has lost its attaching apparatus. It draws itself together into a ball, and encysts singly or in pairs. In the latter case, after

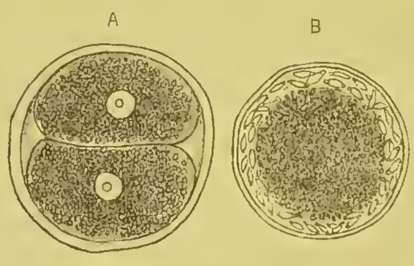


Fig. 96.—Encapsuled Gregarines. (*A*) After conjugation; (*B*) After formation of pseudonavicellæ.

[1] Hence the name *Gregarina*, from "Grex," a herd.

[2] For an account of the Gregarines, properly so called, see especially the researches of Frantzius, "Observationes quædam de Gregarinis," Wratislav, 1846; Stein, "Ueber die Natur der Gregarinen," *Müller's Archiv f. Anat. u. Physiol.*, p. 182, 1848; and Aimé Schneider, "Contribut. à l'hist. des Grégarines," *Archiv. d. Zool. expér.*, t. iv., p. 493 *et seq.*, 1875.

the conjugation has taken place, the two bodies are still distinguishable within the wall of the cyst (Fig. 96, *A*), after this the contents, either as a whole or in their outer layer, produce by a sort of peripheral segmentation a large number of small balls, which become the spindle-shaped Pseudonavicellæ after the secretion of a hard shell (Fig. 96, *B*).

We cannot here discuss the numerous more or less striking differences in the form and size of these spores. We must, however, point out that the cysts sooner or later find their way to the exterior (though often, as in the earthworm, only after the death of their host), and there set the spores free. For this last purpose there are sometimes special arrangements in the cysts, such as canals and "discharging bombs," which are formed out of that portion of the contents which was not devoted to the manufacture of spores.[1]

Each Pseudonavicella contains a granular mass, which, after secreting a clear plasma, very soon gathers itself into a central mass. According to Lieberkühn, who bases his statement on investigations into the Gregarine of the common earthworm (*Monocystis agilis s. lumbrici*), this mass forms an amœboid creature, which breaks out of the Pseudonavicella, remains for a while in the body-cavity of its host, and finally becomes a Gregarine by the assumption of a cuticle.[2]

It is, however, hardly doubtful that Lieberkühn has fallen into error. He has confused amœboid masses found in the perivisceral fluid of the earthworm, and representing blood or lymph corpuscles with stages in the life-history of the Gregarine. He has also further erred in regard to the changes which the contents of the Pseudonavicellæ undergo, for, especially in the case of *Monocystis lumbrici*, it is certain, as Schneider has stated, that the development is quite otherwise. The contents, instead of forming an amœboid body, fall into about six little clear sickle-shaped rods. These distribute themselves equally over the two halves of the Pseudonavicella, and the rest of the granular mass collected into a ball lies between them ("nucléus de reliquat").—(Fig. 97, *A-C*.) The same changes take place also in many other Gregarines, usually, however, not in the original host, but externally. The expelled cysts may be kept alive for some weeks in water (Fig. 97, *D-F*).

Since Schneider succeeded, after treatment with osmic acid, in demonstrating the presence of a nucleus in the sickle-shaped bodies, he supposes that they are already true Gregarines, and that they pass without essential change, by growth, accumulation of

[1] Aimé Schneider, "Sur un appareil de dissémination des Grégarines," *Comptes rendus*, t. lxxx., p. 432, 1875.

[2] "Evolution des Grégarines," *Mém. couronn. de l'Acad. de Belge*, t. xxvi., 1855.

granules, and secretion of a firm cuticle, into the adult Gregarines. With this agree the observations of A. Schmidt,[1] who found the first stages of *Monocystis lumbrici* as extremely small, transparent, membraneless creatures within the spermatic vesicles of the host, and who also

FIG. 97.—Pseudonavicellæ with germinal rods in their interior; *A-C*, of *Monocystis agilis; D* and *E*, of *Urospora nemertidis; F*, of *Gonospora terebellæ* (after Aimé Schneider).

attempted to follow their further development. Such a Gregarine is sometimes so small that it hardly attains a third of the diameter of the vesicle, but is in other eases so large as completely to fill it, and even to distend it beyond its usual dimensions.[2] The sperm cells, which are situated outside the infected vesicles, have obviously a somewhat abnormal development in consequence of parasitism, showing, instead of long threads, a short tufted fringe, which persists for a while on the periphery of the young Gregarine,[3] and is only thrown off after they creep out.

According to the younger van Beneden,[4] the development of *Gregarina gigantea,* which lives in the intestine of the lobster, and sometimes attains a length of 16 mm., is somewhat less direct. Instead of passing directly into the Gregarine form, the amœboid mobile stage produces two long bud-like processes, which then pass into Gregarine forms, which are at first destitute of a nucleus.

We must leave it to the future to decide between these contradictory opinions,[5] and will only further state that, according to Schneider, there are also Gregarines whose Pseudonavicellæ, instead of the

[1] "Beitrag zur Kenntniss der Gregarinen und deren Entwickelung," *Abhandl. d. Senkenberg. Gesellsch.*, Bd. i., p. 168 *et seq.*, 1854.

[2] See the confirmatory researches of Lieberkühn, *Müller's Archiv f. Anat. u. Physiol.*, p. 509, 1865.

[3] Such structures have given occasion to the opinion that there were (in the earthworm) *Gregarinæ* provided with bristles.

[4] "Recherches sur l' évolution des Grégarines," *Bull. Acad. roy. Belg.*, t. xxxi., 1871. [Translation, *Quart. Journ. Micr. Sci.*, N. S., vol. xi., p. 242, 1871; also *Ann. Mag. Nat. Hist.*, ser. 4, vol. x., p. 309, 1872.—W. E. H.]

[5] [The number of these rival theories has recently been increased by Ruschhaupt (*Jenaisch. Zeitschr.*, Bd. xviii., p. 713, 1885), who does not regard the sickle-shaped bodies in the Pseudonavicellæ of the Gregarines as true nuclei, but rather considers that the young Gregarines arise from the general mass of the Pseudonavicellæ.—R. L.]

above described rods, contain a perfectly clear protoplasm, or are filled with a uniformly granular substance, in which one can sometimes distinguish a nucleus.

With these Gregarines are associated, as Leydig[1] first showed, the so-called "Psorosperm-saccules," discovered by J. Müller.[2] These are parasitic organisms of varying shape, some microscopic, some several millimetres across, found often abundantly in the most diverse situations on the bodies of fishes and frogs (*e.g.*, on the skin, gills, and in the muscles, kidneys, or urinary bladder). To the naked eye, they appear as small white points or sacs. Their close relationship with the Gregarines is proved by the nature of the contents, which consist of hard-shelled Psorospermiæ, exactly like the Pseudonavicellæ. They only differ from the latter in minor characters, as the presence of a tail-like process of the shell, such as is also seen on the eggs of some ectoparasitic Trematodes (p. 45).

Yet it seems hardly allowable to class these Psorosperm-saccules[3] along with the Gregarines. For not only have they no capsular wall, like that surrounding the group of young Pseudonavicellæ, but further, the formation of the Psorosperms generally begins at a time when the organisms have not yet attained their full size, and goes on throughout the whole subsequent life. What takes place in the Gregarines in two successive stages, is in the Psorosperm-saccules distinct neither as regards space nor time.

And, besides the fact that the formation of Psorosperms takes place without previous encystation, it must also be noted that the resulting organisms have not the nucleus and firm cuticle of the Gregarines. They appear as simple masses of protoplasm with scattered fatty granules. Their power of motion is also more limited, and is in some cases, especially in the later stages, hardly perceptible. They manifest their activity generally only in protrusion and retraction of a part of their body-substance.

The formation of Psorosperm-saccules is effected thus—the original uniformly granular substance gradually becomes a mass of distinctly defined balls (Fig. 98), which become surrounded with a transparent covering, and then become single or double Psorosperms. These pass away almost as soon as they are formed, and appear in all cases to have a further development, so that their contents have usually a different character from that of the ordinary Pseudonavicellæ. In some

[1] "Ueber Psorospermien und Gregarinen," *Müller's Archiv f. Anat. u. Physiol.*, p. 221, 1851.

[2] "Ueber eine eigenthümliche krankhafte parasitische Bildung mit specifisch organisirten Samenkörperchen (Psorospermia)," *ibid.*, p. 477 *et seq.*, 1841.

[3] Our knowledge of the Psorosperm-saccules rests specially on the researches of Lieberkühn, *Müller's Archiv f. Anat. u. Physiol.*, pp. 1-24 and 349-368, 1854.

cases indeed, as Lieberkühn observed in those inhabiting the kidneys of the frog, the contents fall into rod-like transparent bodies exactly like the Pseudonavicellæ of the earth-worm Gregarine. Here also three to five of these rods usually have a granular ball lying between them, and in one case Lieberkühn saw these rods in distinct motion. They not only glided slowly up and down the wall of the Psorosperm, twisting and bending to suit the form of the interior space and forcing the granular mass now here now there; they also swelled up into a globular form so as almost to fill the whole shell. The latter suddenly burst, and the contents thus escaped, first the granular ball, then the transparent rods, the latter also in spherical form and exhibiting amœboid movements for a short time. The empty shells were very commonly found, and in the kidneys of the infected frogs numerous amœboid bodies were to be seen, some of which were quite identical with the free creeping transparent balls, while others enclosed finer and coarser granular contents, and passed through all the intermediate stages, leading finally to Gregarine parasites. All this led Lieberkühn to conclude that the young brood grew to maturity within the original host.

Fig. 98.—Psorosperm-saccule from the urinary bladder of the pike (after Lieberkühn).

It is, however, still doubtful how far the occurrence of these hyaline rods is constant among the Psorosperms. In the majority of cases, and in the common Psorosperms of fish, the interior of the shell is filled with a clear homogeneous mass, near which, however, there are two elliptical so-called "polar bodies" at one end (Fig. 99, *A*). One might perhaps suppose that these are contracted rods, but according to the observations of Balbiani[1] and Schneider,[2] they appear as vesicles enclosing an exceedingly long and fine thread. This is usually twisted in a close spiral, but in some cases stretches out of the shell through a special opening. The meaning of this thread is not known, but this is at least certain, that Balbiani's idea of regarding it as a sperm-cilium has no foundation. It is perhaps to be regarded as an apparatus of fixation. The possibility of regarding these polar bodies as equivalents of the rods, is finally excluded by the fact that the hyaline contents of the Psorosperms finally contract into a spherical mass, which creeps out (when the shell is split in two by

[1] *Comptes rendus*, t. lvii., p. 157, 1863.
[2] *Archiv. d. zool. expér.*, t. iv., p. 548, 1875.

pressure) as a mobile amœboid organism (Fig. 99, *B*), as has been repeatedly observed both by Lieberkühn and Balbiani. Since Lieberkühn found these empty shells not unfrequently even within the Psorosperm-saccules, and further saw the latter penetrated and surrounded by amœboid bodies, which agreed perfectly with the hyaline balls previously liberated outside, it is probable that the young parasitic brood sometimes escapes even within the host.

A third group of Sporozoa consists of the so-called "egg-shaped Psorosperms," which are of special interest to us, since they occur as parasites, and, under certain circumstances, as dangerous parasites, in Mammalia, and even in man. They are not, however, by any means confined to the higher animals, for many species are found in Invertebrata, *e.g.*, in the common garden snail, in which a form of this kind was discovered more than twenty years ago by Dr. Kloss in Frankfort, and accurately followed through all its stages.[1] The term "Psorospermiæ," given to these parasites, is of course only slightly suitable, for the body thus denoted is not comparable to a germ or spore, but represents the Gregarinoid mother-animal, inside which the true Psorosperms are

Fig. 99.—Psorosperms, *A*, from the urinary bladder of *Gadus lota*; *B*, from the gills of the bream, the latter split with the amœboid body creeping out (after Lieberkühn).

Fig. 100.—Coccidia from the intestine of the domestic mouse. *A*, inside an epithelial cell, still without a capsule; *B*, *C*, encapsuled with Psorosperm and germ; *D*, *E*, *F*, isolated Psorosperms; *G*, amœboid brood (after Eimer).

afterwards developed. The only thing which recalls the Psorosperms is the firm shell, with which these surround themselves at the close of their period of growth, a structure evidently analogous to the capsule of the quiescent Gregarine, which establishes here also the existence of an encapsuled resting-stage. In this state the parasites so closely resemble the eggs of certain intestinal worms, that they have often been mistaken for them even by experienced microscopists;

[1] "Ueber Parasiten in der Niere von Helix," *Abhandl. d. Senkenberg. naturf. Gesellsch.*, Bd. i., p. 189 *et seq.*, 1855.

and, *vice versa*, true worms have sometimes (by Robin) been regarded as Psorosperms.

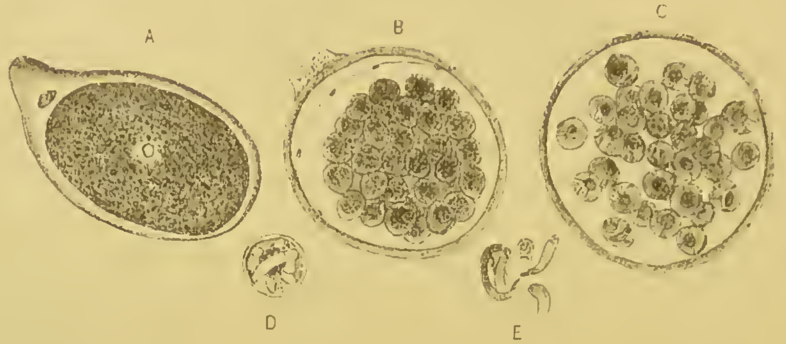


FIG. 101.—Coccidia from the kidneys of the garden snail. *A*, inside a cell, still without a capsule ; *B*, *C*, encapsuled with Psorosperms inside ; *D* and *E*, Psorosperms with germs, in *E*, in the act of exit (after Kloss).

So long as these creatures are destitute of a capsule, they appear as membraneless cells with a distinct nucleus. In this stage, they are usually found inside cells, especially epithelial cells, which they gradually cause to swell up in consequence of their growth, and finally destroy by their exit, which usually occurs after the encystation.

The spores are formed from the granular contents of the *Coccidium*, for by this name we shall henceforth designate the so-called "egg-shaped Psorosperms." They are sometimes few in number, but sometimes many, and they are occasionally very numerous. The former case is described by Eimer[1] in the form observed by him in the intestinal epithelium of the mouse (*Eimeria*, Schn., Fig. 100). The other case is exhibited by the Coccidia of the Mollusca, *e.g.*, *Helix* (*Klossia*, Schn., Fig. 101), or, still better, by those of the cuttle-fish (*Benedenia*, Schn.), which are also infested by these parasites.[2] In *Coccidium oviforme* (Fig. 102), which is of special interest to us, there are, as far as my observations go, always four spores, which are provided as usual with a comparatively thin shell. They only develop after the Coccidia have left the body of the

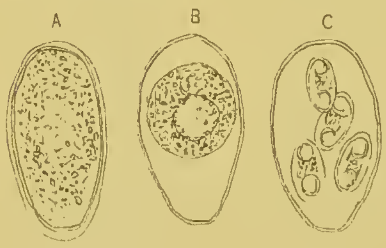


FIG. 102.—*Coccidium oviforme* from the liver of the rabbit. In *C* there are Psorosperms in the interior.

[1] "Ueber die ei- oder kugelförmigen sog. Psorospermien der Wirbelthiere :" Würzburg, 1870.

[2] The cells grow before the formation of spores to a size of above 2 mm. See observations of Eberth, *Zeitschr. f. wiss. Zool.*, Bd. xi., p. 397, 1862; and Aimé Schneider, *Archiv. d. zool. expér.*, t. iv., p. 40, 1875.

host, and have lived for sometimes weeks or months in the water, while in ordinary cases they are formed soon after the encapsulation, or at least while yet inside the host. The shape of spore, so characteristic of the Gregarines and Psorosperm-sacculcs, is here replaced by a simpler spherical or ovoid form.

Along with the spore-formation there occurs simultaneously the development of the embryonic body, which appears throughout to be in the form of a hyaline sickle-shaped rod. Adjoining these, the usual granular body (" nucléus de reliquat ") is present with equal constancy. The number of rods varies, but is generally from six to eight (Fig. 100, *D-F*; Fig. 101, *D, E*). *Coccidium oviforme* always forms only a single rod,[1] which lies on the granular mass (Fig. 102, *C*).

When these structures attain development in the body of their host, then, according to Kloss and Eimer, one can observe a distinct movement, which, under favourable circumstances, may be watched for hours, and is associated with a manifold change of form (Fig. 100, *G*). When they pass into the quiescent state they assume a more or less compressed, sometimes almost spherical form, although they usually retain a slightly curved shape. Kloss calls the movement " leech-like," and sometimes compares it with the creeping motion of a sluggish *Euglena*.

In this contracted state these rods are in size and appearance so thoroughly identical with the scarcely nucleated youngest stage of the parasites, that (considering the contemporaneous presence and the different number of stages) one can hardly be mistaken in connecting the latter directly with the mobile germs, and crediting the forms in question with continuous multiplication.

Of course this applies only to what may be called the " viviparous " species. When the formation of germs takes place outside the host, as in *Coccidium oviforme*, then the appearance of immense numbers must of course be due to often repeated introduction.

Whether structures somewhat similar to the above, the so-called "Miescher's tubes" (*Synchytrium Miescherianum*, Zopf), are to be referred to the class Sporozoa, is more doubtful, since no phenomena of movement have yet been observed in any developmental stage. Since, however, they are usually ranked with the Psorosperm-saccules, in accordance with a decision which I was the first to give,[2] and have indeed many points of resemblance with these forms, a brief discussion of their nature is necessary. We must confess that our knowledge of

[1] [Balbiani (*loc. cit.*, p. 105) believes that he has proved that the sickle-shaped bodies are double also in *Coccidium oviforme*, but that the two portions lie closely pressed together.—R. L.]

[2] This work, first German ed., Bd. i., p. 240.

them is still very far from satisfactory or complete, although they are of most common occurrence in our domestic animals,—pig, ox, sheep, and even deer.

The first to notice these curious forms was Miescher, who observed the muscles of a domestic mouse penetrated in the direction of the fibres by long strips, visible even to the naked eye, which on closer examination appeared as cylindrical tubes filled with countless minute kidney-shaped bodies.[1] Similar though shorter tubes were seen by Hessling in the muscles of the roe and other Mammalia, and indeed inside the muscular fibres,[2] still surrounded on all sides by the striated sarcous substance. The observations of Rainey, who thought he had in the tubes the first stage of the common bladder-worm of the pig,[3] and subsequent observations of my own,[4] proved that this occurrence inside the muscular fibre was constant (Figs. 103 and 104). They have not as yet been found anywhere else, although numerous observers have in the meantime devoted close attention to them.[5]

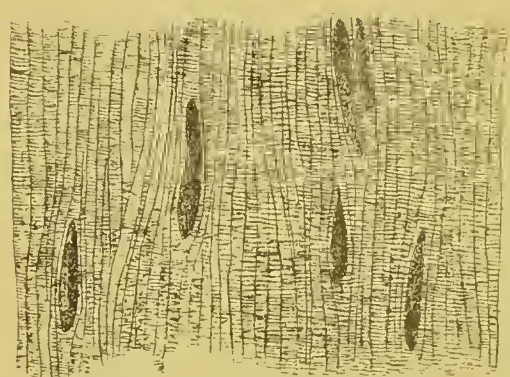


Fig. 103.—Rainey's tubes, enlarged about 40 diameters.

Fig. 104.—One of Rainey's bodies within an isolated muscular fibre, enlarged 100 diameters.

As long as the muscular fibres have their normal extension, the tubes preserve an elongated form; but this is altered, and gives place

[1] *Bericht über die Verhandl. d. naturforsch. Gesellsch. zu Basel*, p. 143, 1843. Figured by v. Siebold, *Zeitschr. f. wiss. Zool.*, Bd. v., tab. x., Fig. 10, 11, 1854.

[2] *Zeitschr. f. wiss. Zool.*, Bd. v., p. 196 *et seq.*, 1854.

[3] *Phil. trans.*, vol. cxlvii., p. 114 *et seq.*, 1857.

[4] *Loc. cit.*, where Rainey's mistake was corrected.

[5] Of the numerous papers on these organisms, I may specially mention Manz, "Beitrag zur Kenntniss der Miescher'schen Schläuche," *Archiv f. mikrosk. Anat.*, Bd. iii., p. 345 *et seq.*, 1867.

to a more swollen shape, whenever the muscles are loosed from their natural insertion and the fibres contract.

Their boundary wall consists of a somewhat thick and firm cuticle, which (especially in younger, *i.e.*, smaller tubes) is perforated by numerous pore-canals, of course not always equally distinct (Fig. 105). In consequence of certain external influences, the canals are often united together by rupture, and in such cases the cuticle disintegrates into a fringe of rods, as so often occurs also in the cuticular border of the intestinal epithelial cells. Virchow regards these rods as parts of the surrounding sarcous substance,[1] but in this he is mistaken, as are also those investigators who (with Rainey and Rivolta) regard them as cilia, and make them take part in the movement of the organism. Inside the cuticle, embedded in a tough, somewhat homogeneous matrix, lie a countless number of microscopic (0·01 mm.) kidney-shaped or bean-shaped bodies. In their perfectly fresh state these are of a hyaline appearance, containing at most a few sharply defined granules near the ends, and forming after a while a few vacuoles. Independent movements cannot be observed in those bodies, although they exhibit manifold changes of form. In the younger, *i.e.*, smaller, tubes (of only 0·7 to 1 mm.), we find, beside and between the kidney-shaped bodies, numerous round transparent balls, probably to be regarded as the immature stages of the former. These structures are not equally scattered throughout the protoplasm of the tube, but are arranged in groups, enclosed in thin-skinned spheres of about 0·025 to 0·05 mm., which lie together in a closely pressed mass (Fig. 105).

FIG. 105.—Extremity of one of Miescher's tubes with its contents. At the side are the kidney-shaped bodies, much enlarged.

If, in determining the nature of these structures, we seek to follow the analogy of the other Sporozoa, we may consider the balls as spores, and compare the kidney-shaped bodies with the hyaline rods.[2] The latter would therefore be the embryonic stage. Unfortunately we cannot corroborate this plausible hypothesis by positive experimental results. In an experiment which I made, a pig, proved to be free from these tubes, was fed with them, and was afterwards found to be infested with them. But on this I could lay no special emphasis, not only because it was only a single case, but

[1] "Lehre von den Trichinen," p. 23, 1866.

[2] The occasionally slender form of these bodies indeed recalls the rod-like or sickle-shaped reproductive bodies of other Sporozoa. On the other hand, there are also Fungus-spores of very similar shape.

because the infection might have taken place in some other way. Manz asserted his conviction that the digestive juice had a destructive effect on the tubes; and having used some for feeding an animal, he could find, after a few hours, only their remains in the gastric contents; nor was there a trace of them in the intestinal wall or in the muscles.

Although the tubes occasionally occur in immense numbers close to one another, so that the flesh looks as if half of it consisted of Psorosperm-tubes, yet they seem usually to cause no special uneasiness. In many cases, however, the phenomena of paraplegia, retarded respiration, and even suffocation, are observed as associated with the presence of the tubes, and may with some probability be referred to this cause (Damann, Leisering, v. Niederhäusern).

These parasites have, however, no bearing on human pathology, for in spite of their frequency and wide distribution (not even the common fowl being exempt), they have never as yet been found in man. Even the eating of flesh containing Psorosperms in abundance has hitherto always proved harmless.

Having become somewhat familiar, through the foregoing information, with the general structure and life-history of the parasites belonging to the Sporozoa, it is time to become acquainted more in detail with the occurrence of these creatures in man. We shall therefore turn to the consideration of the so-called "egg-shaped Psoroperm," of which mention has already been made.

Coccidium, Leuckart.

Kloss, "Ueber Parasiten in der Niere von Helix," *Abhandl. d. Senkenb. Gesellsch. Frankf.*, 1855.

Eimer, "Ueber die ei- oder kugelförmigen sog. Psorospermien der Wirbelthiere." Würzburg, 1870.

Aimé Schneider, "Note sur la psorospermie du poulpe," *Archiv. d. zool. expér.*, t. iv., p. xl., 1875.

In their youth, these parasites are naked inhabitants of epithelial cells, but afterwards envelop themselves with a firm shell at the close of their period of growth. In this condition, in which they present a puzzling resemblance to the eggs of certain Entozoa, they quit their former resting-place, and generally the former host also, and transform their substance into a larger or smaller number of spores, each having a granular ball and rod within. The spores themselves have a rather thin wall, and are of a round or elliptical shape.

We have already observed that the *Coccidia* occur preferably in warm-blooded organisms, and that they sometimes appear in such

enormous numbers, especially in the intestine and in the bile-ducts, as extensively to destroy the epithelial cells, and produce pathological changes of a very remarkable nature. Of all this family, *Coccidium oviforme,* which we are about to describe, has been longest known and most frequently observed, and is also the only one which has hitherto been observed in man.

Coccidium oviforme, Leuckart.

Kauffmann, "Analecta ad tuberculorum et entozoorum cognitionem," Dissert. inaug., Berolini, 1857.

Lieberkühn, "Ueber die Psorospermien," *Müller's Archiv f. Anat. u. Phys.*, p. 7, 1854.

Idem, "Evolution des Grégarines," *Mém. couronn. de l'Acad. de Belge, loc. cit.*, pp. 26-34, 1855.

Stieda, "Ueber die Psorospermien der Kaninchenleber und ihre Entwicklung," *Archiv f. pathol. Anat.*, Bd. xxxii., p. 132, 1865.

Reincke, "Nonnulla quædam de psorospermiis cuniculi," Dissert. inaug., Berolini, 1866.

Waldenburg, "Zur Entwicklungsgeschichte der Psorospermien," *Archiv f. pathol. Anat.*, Bd. xl., p. 435, 1867.

Rivolta, "Psorospermi e psorospermosi," *Medico Veterinario Torino,* t. iv., No. 2, 1869.

Idem, "Dei parassiti vegetali," p. 381 *et seq.:* Torino, 1873.

Egg-shaped bodies, 0·033 *to* 0·037 *mm. long and* 0·015 *to* 0·02 *mm. broad, with thick smooth shells, which have a micropylar opening at one end, usually the narrower. The granular contents are sometimes uniformly distributed throughout the whole interior space, or sometimes, as in the more globose forms, collected into a spherical mass* (0·017 *mm.*). *In this state the parasites pass from the liver and intestine which they inhabit to the exterior, there to undergo a further development in the moist surroundings. The contents thereupon segregate into four oval spores* (0·012 *mm. long,* 0·007 *mm. broad*), *which become surrounded with a but slightly firm coat, and form each a single* C*-shaped curved hyaline rod, the concavity of which is occupied by closely packed granules.*

The liver of the rabbit (Fig. 107) is not unfrequently found penetrated with white nodules, which, in more or less considerable numbers, grow gradually to the size of a hazel-nut, and excite painful affections, in the course of which the animal often dies. In many warrens the disease becomes a serious epidemic, so that hardly a single healthy animal is to be found. On section of the nodules a cheesy or purulent, sometimes yellow-coloured, mass exudes, in which a microscopic examination reveals, besides cell *débris*, a countless number of the above-described oval bodies. Since the same structures are also found at the same time in the gall-bladder, it may also be concluded that the nodules are in association with the bile-duct.

These nodules are so like pseudoplasmic deposits that we can understand how the first observers regarded and described them as such.

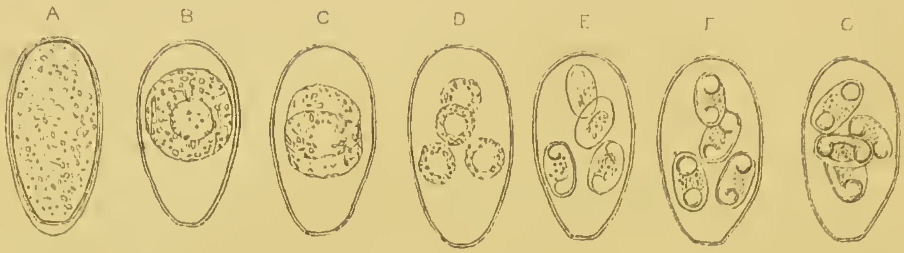


Fig. 106.—*Coccidium oviforme*, from the liver of the rabbit (× 550). *C-G*, stages of spore-formation only observed in the free state.

Carswell considered them to be tubercles, and Hake,[1] who was the first to examine them more minutely, regarded them as carcinomata. They were thought to have arisen from degeneration of the bile-ducts, and to enclose numerous pus-corpuscles of peculiar form. Nasse[2] contradicted Hake's conclusion, and thought that the "pus-corpuscles" should be regarded as abnormally altered epithelium. He compares them to cartilage-cells, and urged that "the epithelium of the bile-duct of sheep is sometimes found ossified, namely, when the sheep are infested with *Distomum*."

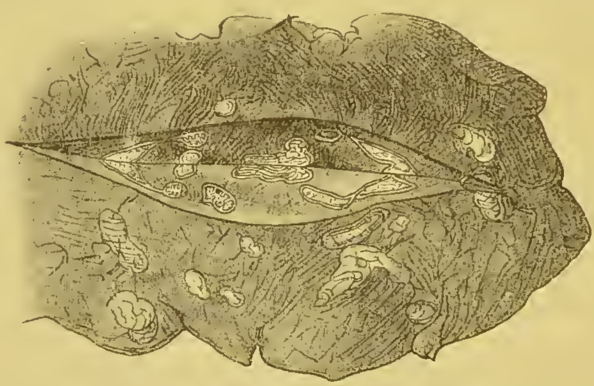


Fig. 107.—Liver of a rabbit with *Coccidium*-nodules.

The true nature of these bodies long remained uncertain, although Remak[3] pointed out the resemblance between these structures and the Psorosperms just discovered by Joh. Müller, and asserted their close

[1] "A treatise of varicose capillaries, as constituting the structure of carcinoma of the hepatic ducts, with an account of a new form of pus globuli:" London, 1839.

[2] "Ueber die eiförmigen Zellen der tuberkelähnlichen Ablagerungen in den Gallengängen der Kaninchen," *Müller's Archiv f. Anat. u. Physiol.*, p. 209 *et seq.*, 1843.

[3] "Diagnostische und pathologische Untersuchungen," p. 235: Berlin, 1845.

relationship. Kauffmann[1] corroborated this, and tried to prove the biological independence of the cells by observing that the enclosed granular masses, after being kept for a while in water, broke up into four parts, and became new Psorosperm-like bodies. Arguments have been constantly brought forward, down to our own day, in favour of the theory that these bodies were pathologically altered cells,[2] and all the more so when it was established that they occurred by no means exclusively in the rabbit's liver, but not unfrequently in other animals and in other organs, especially in and upon the intestinal epithelium. On the other hand, the *Coccidia* were often regarded as eggs of Entozoa, such as Distomes, and particularly *D. lanceolatum;* and, indeed, their resemblance to the latter is on superficial inspection very striking, for the size and appearance of the shell are identical, and the micropylar opening recalls the little lid on the Distome-egg. More minute examination of fresh specimens will, however, at once reveal the characteristic differences.

With our present knowledge the nature of the egg-like bodies is no longer a doubtful matter. The changes which they undergo after they leave the body of their host, and the development which takes place within the epithelial cells only admit of one explanation, that, namely, which regards them as Gregarinoid parasites.[3]

Considering the importance of the intracellular occurrence of *Coccidium,* we may perhaps note that it was Remak who first established it. The fact has been confirmed, but only for the intestinal *Coccidium,* by Klebs[4] and others (Waldenburg, Reincke, Neumann, Eimer). For our knowledge of the spore-formation we are indebted to Kauffmann, who first observed it, and also especially to Stieda and Reineke.

Structure and Development.

When one examines *Coccidia* fresh from the so-called "Psorosperm-nodule," it is easy to distinguish (Fig. 106, *A*, *B*) two different forms.

[1] *Loc. cit.*, p. 17.

[2] See among others Lang, *Archiv f. pathol. Anat.*, Bd. xliv., p. 202, 1868, and Roloff, *ibid.*, Bd. xxxiii., p. 512. I must not conceal that I myself for a while supported this erroneous opinion. It originated in the observation of a case in which a dog infected with *Trichinæ* showed an intestinal membrane much altered by Helminthiasis, and covered throughout its whole extent with a thick layer of egg-shaped *Psorospermiæ*. See my work on *Trichina*, first edition, p. 11, 1860.

[3] Among the investigators who have specially studied the developmental history of *Coccidia*, Stieda alone dissents. His opinion regarding the *Psorospermiæ*, and especially those inhabiting the liver of the rabbit, is that they are "very early stages of as yet unknown animal parasites." I will in this connection only note that Stieda has not seen the occurrence and development of *Psorospermiæ* within cells.

[4] "Psorospermien im Innern von thierischen Zellen," *Archiv f. pathol. Anat.*, Bd. xvi., p. 189, 1859.

The one is more slender, and filled with uniformly diffused granular contents; the other is thicker and provided with a granular ball, which has a diameter of 0·017 mm., and lies in the middle of the internal space, leaving a great part of it free. The latter contains a clear fluid, which is easily coloured by staining fluids, and acquires in time a somewhat firm consistency. One can not unfrequently recognise in the granular mass of the ball another clear sphere of varying size, which one would at once consider as a nucleus if it were more sharply defined and allowed itself to be stained. In point of fact, however, it can hardly be otherwise described than as a drop-like aggregation of the clear ground substance which connects the granules together. I have never been able to find a genuine nucleus.

The appearance of the contents exhibits many other differences in detail. In the majority of *Coccidia* it is throughout of a finely granular nature, but in other cases the protoplasm contains a more or less considerable number of coarser granules, which are strongly refracting, and not unfrequently flow together into larger masses like fat-granules. Since *Coccidia* thus altered are much more common among forms which have been cultivated than in fresh material, and since I have never observed them to undergo any further change, I conclude that they are dead specimens. The distinctively greater narrowing of one end is hardly noticeable in the slender forms, and similarly the so-called micropyle is for the most part, and that constantly, found in those of bulging shape. Even the character of the shell varies, and is not unfrequently double (Fig. 106, *A*), in the slender *Coccidia*. The outer wall is thinner than the inner, which agrees exactly with the shell of the bulging forms, both in its appearance and in its micropylar arrangement. Since there are also specimens in which the outer shell is represented only by a delicate more or less distant border, and others which are provided only with a simple completely closed shell, this lends some support to the opinion that the *Coccidia* in certain developmental stages cast their skin, and afterwards assume the bulging form, with micropyle and central mass of granules (Fig. 106, *B*). If we regard this shell (which is provided with a micropyle, and perfectly resembles an egg-shell in its refractive power and double contour) as a kind of capsule, then the previous thinner coating may perhaps represent the true cuticle. However, the fact that the capsule wall would then arise under the cuticle, and not from it, as in the Gregarines, seems hardly in favour of this opinion.

The formation of the body here described does not take place freely in the interior of the enlarged bile-duct, but in its epithelial lining. Although Stieda declared that he had never seen such a mode of origin, and Waldenburg affirmed the same in regard to the

Psorosperms from the liver, and although, on the other hand, others (Vulpian, Roloff) have claimed the liver cells themselves as the germs of the *Coccidia*, there can be no doubt of the above fact. Every well prepared cross section furnishes convincing proof[1] (Fig. 109).

The wall of the *Coccidium*-nodules consists of a thick firm mass of connective tissue with frequent nuclei and fibres, usually arranged concentrically. Besides numerous blood-vessels, one can not unfrequently recognise, especially towards the periphery, smaller and larger groups of liver-cells and of bile-ducts, which, although enlarged in varying degrees, may be only slightly changed and often still contain a regular columnar epithelium.

We might perhaps explain these appearances by supposing that the connective tissue wall increases continually in thickness at the expense of the liver substance, while the adjacent acini proliferate and are crowded together in an ever widening circle.[2]

This proliferation of the connective tissue takes place not only outside the nodules, but extends also along the duct into the remoter recesses. Where the acini are usually found crowded in close layers, one finds in the diseased liver numerous bands of connective tissue of varying thickness, which are embedded between the lobules. These enclose a number of bile capillaries, which are often separated from one another only by thin septa, but here and there include little areas of the liver substance between them. These are essentially the same changes as are observed in cases of severe hepatic cirrhosis, except that in the latter the degeneration is restricted to this stage of development, while here it goes further, inasmuch as at certain points where the *Coccidia* have nested the bile-ducts widen and thus occasion the formation of new nodules. Thus also it happens that the cysts are often associated together, and can sometimes be extracted from the liver as a root-like branched system of varicose cords.

At first sight these *Coccidium*-nodules may be seen to be utterly different from the bile-ducts, even from those which were enclosed in the bands of connective tissue. They have not only a wide saccular

[1] I can only explain the opposite opinions by the supposition that the investigators have neglected to make sections of sufficient fineness.

[2] Thus we understand the repeatedly expressed opinion that it is the acini which represent the proper source of the disease. Thus Roloff (*Archiv f. pathol. Anat.*, Bd. xliii., p. 522) states that the nodules arise by exuberant growth of the connective tissue in and between the liver lobules, and that they change into *Coccidia* internally. Lang (*ibid.*, Bd. xliv., p. 202) refers the commencement of the disease to the liver lobules, and describes it as a proliferation of cells, which takes place around the interlobular vessel, and gives rise at once to the destruction of the glandular tissue and the formation of a fibrillar connective tissue, which afterwards undergoes a retrograde metamorphosis from the centre outwards, and thus produces the *Coccidia* partly from the alteration of the cells grouped together in nests resembling cords.

cavity, with the above-described caseous or cream-like contents, but they have further no columnar epithelium. This has been replaced by more or fewer round cells, which lie in a thick layer on the connective tissue sheath, and resemble round granules in appearance (Figs. 108 and 109). This is especially true of the larger cells, which measure 0·03 mm. and more in diameter, and not unfrequently project more or less above their surroundings.

Another difference consists in the fact that the connective tissue clothed with these cells is not only pushed out into numerous recesses, but is also raised into folds, which run longitudinally and often intrude far into the inner space. In some places it is so much occupied by these inwardly projecting folds that there are left only one or two usually peripheral lateral spaces (Fig. 108).

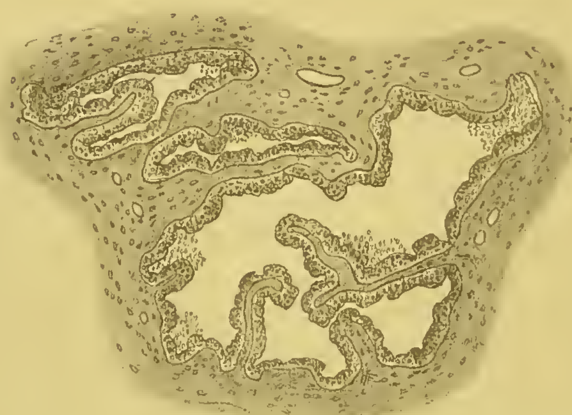


Fig. 108.—Cross section of a *Coccidium*-nodule, slightly enlarged. The contents have been for the most part washed out.

On cross section the folds are very like papillomatous elevations, especially when they are low and, as sometimes happens, forked like a Y. It is thus not difficult to understand how they have been hitherto very generally described as such. Many of them may indeed represent exuberant growths of this kind, but the majority are undoubtedly nothing but the remains of the septa that separated the bile-ducts which were originally more numerous. It is a mistake to refer the nodules to a single much-distended bile-duct for the nature of their origin, as above described, and the character of the intermediate stages, show them to be formed from several closely connected bile-ducts, which, being similarly altered, may gradually coalesce through the more or less perfect disappearance of the dividing walls; and we need not point out how the presence of the side-chambers, hitherto almost entirely overlooked, thus finds its natural explanation.

The intermediate stages, to which we have just referred, furnish

us also with the most convincing evidence that the nodules, in spite of their distention and the very different nature of their contents, are identical with the former bile-ducts. One can see the original columnar epithelium[1] of the latter slowly pass into the above-mentioned cell-masses, and in such a manner that the individual cells, influenced by the pressure and growth of the included *Coccidium*-germs, alter very considerably inform and size. Not only the superficial, but also the deeper epithelial cells share in this change, and the more so since an active cell-multiplication is very often pro-

FIG. 109.—The epithelium of a Psorosperm-nodule, filled with parasites.

gressing simultaneously. As a rule, however, one finds in the larger Psorosperm-nodules considerable spaces with a but slightly altered columnar epithelium (Fig. 109). In other places all likeness to the earlier stage is lost. Here and there the cellular layer is wholly destroyed, so that the connective tissue projects without covering, though the cells are usually replaced by a more or less thick, shining, structureless layer of considerable consistency, and probably of a colloid nature, as Lang has already mentioned.

What I have observed as to the growth of the germs, and the consequent changes of the cells, agrees in the main with the descriptions given by previous observers of the intestinal epithelium cells infected with Psorosperms. I must, however, note that the examination of the intestinal epithelium, as I know from experience, presents less difficulty, and shows the true state of the case on the whole more readily.

The most difficult point, of course, is the demonstration of the newly arrived parasites. I can say nothing definite about them. The smallest germs I was able to distinguish with certainty were slightly granular roundish masses of protoplasm of about 0·009 to 0·01 mm., containing a comparatively large and clear nucleus-like

[1] According to Lang, these columnar cells have been formed anew in the proliferation of the connective tissue, and have then further grouped themselves in tubular nests.

spot (0·005 mm.), which enclosed nucleoli, and was easily distinguished from the cell-contents, though destitute of a special membrane. The form of the enclosing cells varied very markedly, the transverse diameter having grown to double the former size. This change was, of course, still more striking afterwards, for the germ inside continues growing till it finally becomes a spherical ball of about 0·026 mm. In this state the parasite has, apart from the absence of the cuticle, an undeniable resemblance to a Gregarine. Its protoplasm is granular, but always allows the nucleus to be seen glimmering through as a clear spot. It now fills the cell so completely that the latter is seen only as a narrow limiting envelope. I have usually been able to find the original nucleus only in the earlier stages of the parasites.

The number of germs which find their way in is usually so considerable that the cells are generally wholly infected with parasites of different sizes and stages. It is by no means always a single germ which invades each cell,—two are sometimes found together, and occasionally the number is still larger. I have found cells in which I could distinguish five or six granular masses of unequal size lying together.[1]

As soon as the granular masses have attained their maximum size, the transformation into the true *Coccidium*-form begins. The ball, which has still retained its round form, assumes a more oval shape, and surrounds itself under the previous envelope with a rapidly thickening shell. As long as the cell-wall persists, the *Coccidia* lie in or on the walls of the liver-nodules, but later, as we have seen, they are found in the inner space, embedded in a finely granular detritus, with nuclei, remains of cells, and shed epithelial elements.

FIG. 110.—Adult *Coccidia* from the liver.

We have already described (p. 206) how these *Coccidia* (Fig. 110) change during their stay in the liver. We know that the definitive shell, with its micropyle and double contour, subsequently appears under the original primordial coat,[2] and that the granular protoplasm within rolls itself up into a ball in the middle of the capsule.

[1] Waldenburg and Rivolta account for several germs within one cell (seen also by Klebs, Reincke, and Neumann), not by a repeated immigration, but by a division of the original occupant.

[2] I may here expressly note that this assertion rests on no confusion with the remains of the cells which lie immediately round the *Coccidia*, for the casting of the skin can sometimes still be observed in specimens which have been kept for some time in water. On the other hand, the representations which Lieberkühn makes of *Coccidia* with double walls obviously refer (since sometimes two or three *Coccidia* are lying within the same envelope) to specimens still within their epithelial cells ("Evolution des Grégarines," *loc. cit.*, p. 33).

I have never been able to observe any further change in the *Coccidia* within their host. A like want of success has attended most of the earlier observers of *Coccidia* in warm-blooded animals, and that whether the germs originated in the liver or in the intestine. The only one who reports differently is Eimer; but the object on which he bases his results is plainly different from *Coccidium oviforme*, and cannot be directly ranked with it, as we shall afterwards see.

But the *Coccidia* do not remain permanently in their hosts. They pass, though indeed only to a small extent, through the communications which persist here and there between the nodules and the bile-ducts, and reach sooner or later the gall-bladder and intestine, and are finally expelled with the fæces, just as are the parasites and eggs directly developed in the intestine. Having reached the exterior, they undergo, like the eggs of worms (p. 54), a further development, after a longer or shorter period of incubation. This was first discovered by Kauffmann (1847), and since then closely studied, especially by Lieberkühn, Stieda, Reincke, and Waldenburg.[1] The results of the last two investigators (except the later experiments of Waldenburg) apply not to the so-called hepatic Psorosperms, but to the *Coccidia* of intestinal epithelium; but these, unlike Eimer's specimens, are forms which exactly coincide with *Coccidium oviforme* in all essentials, if they be indeed a distinct species.

The length of the period of incubation varies in individual cases. Kauffmann observed *Coccidia* kept in water develop after fourteen days, Stieda only after six weeks, and Leiberkühn after months, while Waldenburg and Reincke found *Coccidia* forming spores after a lapse of four to five days, or less. My own cultivation-experiments, which began early in February, furnished, in about a month (in a warm room), the first specimens with Psorosperms. At first there were only a few, but they increased in the course of the following weeks, and towards the end of March the majority of the *Coccidia* had undergone their metamorphosis. The others, which were mostly young forms, with their protoplasm still diffuse, seemed to be dead. But all this was in only one of my cultivations. In other bottles, which stood in a cooler place, only a few specimens attained further development even after nine weeks, although they still seemed, with few exceptions, quite healthy.

Like the hard-shelled worm-eggs, the *Coccidia* have very considerable power of resistance, so that neither chromic acid nor chromate of potassium, of ordinary strength, seem to have an in-

[1] Even in 1862 Waldenburg abandoned his early, undoubtedly somewhat imperfect, observations. See his paper, "Ueber Strucktur und Ursprung der wurmhaltigen Cysten," *Archiv f. pathol. Anat.*, Bd. xxiv., p. 149, 1862.

jurious effect on them. Indeed, it has been stated that their development proceeds more rapidly in these solutions than in water, but this certainly seems to me to require further corroboration.

Whether it be by chance or not, the shortest period of incubation has been as yet exclusively observed in intestinal *Coccidia.* Waldenburg, in the later experiments which he made with hepatic *Coccidia,* was, like the others, unable to observe further development till after the lapse of weeks or months. He thinks it possible that the chromic solution with which he treated his objects might possibly penetrate the intestinal walls more easily and more thoroughly than the masses of liver; but the insufficiency of this explanation was shown by the fact that isolated hepatic *Coccidia,* though far more accessible to external influences than the *Coccidia* of the intestinal epithelium or Lieberkühnian glands, yet required hardly any shorter time for their development.

The changes which occur in the free-living *Coccidia* (Fig. 111) are concerned, as we have previously noted, with the production of spores —the only structures which we can compare with the Psorosperms of allied organisms, and which we might designate by the same name if we wished to use the word in connection with *Coccidia.* Kauffmann declares that these Psorosperms agree with the parent *Coccidia* in everything but size; but Lieberkühn has already justly condemned this statement. The Psorosperms are not only much smaller (0·012 mm.) than the *Coccidia,* but are in their organization hardly less divergent than is the case in the other Sporozoa. The insufficient microscopic power used must certainly be to blame for Kauffmann's mistake.

He has, on the other hand, observed with perfect accuracy that the spores originate by division of the central granular mass. It only rarely happens, indeed, that the actual division [1] is seen, but that only proves that it takes place with great rapidity. In the cases I have observed the four parts can always be distinguished [2] in the granular ball, even when this is still a coherent mass; so that I must leave it undetermined whether a division into two first occurs, or whether the four spheres are present from the beginning. Along with the granular mass the clear plasma inside also divides, so that at the close of the process four segmentations-pheres are found inside the shell, which differ (Fig. 111) from the former central mass in their smaller size (0·009 to 0·01 mm.).

[1] Waldenburg says he has sometimes observed this segmentation while the *Psorospermiæ* were yet in the liver.

[2] I have always found four segmentation spheres and four Psorosperms, never more nor less, although many observers report two or three. Cases of an apparently smaller number are always optical illusions, in which two Psorosperms lie upon and obscure one another.

But these segmentation-spheres very soon assume another shape, changing from a spheroidal to an ovoid form, and pressing to the side the clear plasma which was formerly wholly surrounded by the granular mass, and which had also been increasing at the expense of the latter. The substance of the segmentation-spheres undergoes a further differentiation, and produces finally a transparent curved C-shaped rod. A thin, but tolerably firm, surrounding envelope is at the same time secreted. The rod lies with its convex surface on this above-mentioned envelope, while its concavity embraces the remainder of the granular mass, drawn together into a minute ball (0·005 to 0·006 mm.), and presenting the appearance of an embryo and its yolk-sac (Fig. 112). I have no scruple in regarding the latter as the so-called "nucléus de reliquat," and the rod as the proper reproductive body.

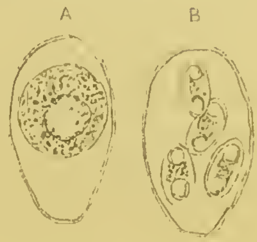


FIG. 111.—Development of Psorosperms in *Coccidia*.

The description which Stieda gives of these Psorosperms is in perfect harmony with my observations. I must specially note my agreement with him on this point, that the rod consists of a uniform, perfectly hyaline substance, and is swollen at its ends into a strongly refracting ball, which perceptibly exceeds the diameter (0·003 mm.) of the connecting part. When this connecting part lies in the direction of the optical axis, as not unfrequently happens, one sees only the two terminal knobs of the rod, which, with the intermediate granular ball, form the figure described by Lieberkühn,[1] according to whom the contents of the *Psorospermiœ* consisted of two transparent polar bodies, separated by a granular ball. This view is of course dissipated when the object is seen from the side.

The newly formed rods (Fig. 112, *B*) have by no means that strong refractive power which they afterwards acquire. Even the little heads are still feebly lustrous, and present essentially the same appearance as the plasma enclosed in the former segmentation-spheres.

The representation which Reincke gives of the rods differs in so far as he denies their homogeneous nature, and describes three or four "globuli cœrulei in modum ceræ lucentes," lying behind one another, which are sometimes so large that they fill up the whole diameter. Two of these structures represent the heads of the rods; the others the thinner median portion.

I have seen forms which bore out the above description, in so far as the heads sometimes seemed as if disjointed, and the median

[1] *Müller's Archiv f. Anat. u. Physiol.*, p. 8, tab. ii., Fig. 37, 1864.

part displayed two segments lying one behind the other, although all the parts were meanwhile still joined together by a slightly refractive connective substance. I do not, however, believe that these objects represent the normal state, not only because they only appeared in my infusion when the number of *Coccidia* containing Psorosperms had increased, but also because they are the prelude to an almost visible destruction of the germs, the details of which will be afterwards summarised.

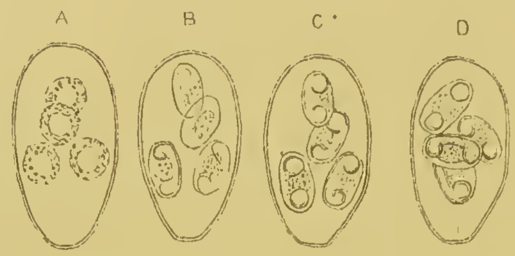


FIG. 112.—*Coccidia* enclosing Psorosperms.

Nor can I agree with Reincke in saying that the Psorosperms are without an envelope, and that it is only the boundary of the rods which sometimes presents this appearance. If Reincke had ever made the experiment of bursting the shells of *Coccidia*, and pressing out the Psorosperms, he would have had no further doubt as to the existence of the envelope. It is, as we have said, a thin but sharply defined and tolerably firm membrane, bearing a little knob, as Stieda mentions, at its sharper extremity.

The clear substance still contained in the interior of the *Coccidia* seems to be of a somewhat consistent nature, as may be concluded from the fact that the Psorosperms only rarely change their position under pressure of the cover-glass. One can sometimes further observe (Fig. 112, *D*) a sharply defined line running down the middle from the micropyle, which looks just like a fold or narrow canal, which is hardly possible in such a fluid plasma.

At this stage the development of the *Coccidia* is for the meantime, in my opinion, complete. Like the eggs of Entozoa containing embryos, they await an opportunity to gain access into a new host, and this opportunity can hardly fail, for the *Coccidia* brought to the exterior with the fæces undergo exactly the same changes in the rabbit warren as in our glass vessels, and will therefore rapidly populate these places with countless germs.

Unfortunately I have not yet had opportunity of proving the possibility of infection by these *Coccidia* and their *Psorospermiæ*, and thus of establishing a supposition, which is rendered highly probable by

all that we know of the reproductive processes of related organisms. This blank has, however, been filled up by other experiments conducted by Waldenburg[1] and Rivolta,[2] who, by feeding with *Coccidia* containing *Psorospermiæ*, produced new *Coccidia*. Rivolta expressly remarks that the presence of the *Psorospermiæ* is an essential condition of success, since *Coccidia* with unsegmented contents remained without change in the alimentary canal of the animal experimented upon. Since Rivolta experimented on fowls, and since the *Coccidia* of these animals represent a distinct species, let us restrict ourselves first to an experiment of Waldenburg's, made on a rabbit four weeks old, and of healthy stock.

Use was made of intestinal *Coccidia*[3] with their contents divided into four, and still in their original place of formation—that is, in the harbouring organs. On the fourth day after feeding there were found on the surface of the intestinal mucous membrane not only a few small mature "*Psorospermiæ*" (*i.e.*, *Coccidia*), but also "numerous round distinctly nucleated bodies, with a fine, often indistinct, membrane, and granular contents lying closely upon it,"—bodies in fact perfectly resembling the young *Coccidia*, usually found enclosed in the epithelial cells. Control observations made on other rabbits born and bred with the one experimented on gave a negative result. As to finding the parasites free on the mucous membrane of the infected animal, Waldenburg concludes that immigration "into the epithelial cells is by no means necessary for the development of the *Psorospermiæ*, especially since in other cases one only finds a comparatively small number shut up in the cells."

Against this statement a subsequent conclusion of Waldenburg's must be placed, although he still upholds the cogency of his feeding experiment. By cultivation of liver-*Coccidia*, he was convinced that the series of changes undergone by the parasite in its free life is by no means terminated by the formation of the spores above described. He denies that the four enclosed bodies are *Psorospermiæ*. They are considered as segmentation-spheres, which, beside and in addition to the granular mass, enclose a clear nucleus at the poles. He contends against calling these nuclei the ends of a distinct rod-like body, and would indeed dispute the existence of any such thing.

After some time the number of these nuclei doubles. Within the membrane of the *Coccidium* there then appear segmentation-spheres,

[1] *Loc. cit.*, Bd. xxiv., p. 163.

[2] "Parass. veget.," p. 390.

[3] A careful examination of these fragments was not undertaken by Waldenburg, who at that time was only acquainted with the investigations of Kauffmann. According to the figures, they are normally developed Psorosperms.

with four nuclei arranged crosswise, and containing a granular mass, which lies embedded between the nuclei, and gathers itself around them. Finally, in the last stage of this developmental process Waldenburg observed that the individual segmentation-spheres had each divided into four new spheres, which enclosed a clear nucleus, and had quite the same appearance as the original spheres, though of course smaller. Thus the *Coccidia* contained sixteen small independent bodies, which had resulted from a repetition of the division of the original contents into four.

In these bodies Waldenburg thinks he has at last found the true germs of the *Coccidia.* They still partially cohere in fours, and issuing from the micropyle, or from an accidental breach, they exactly resemble in action and appearance certain bodies which originate in great number in the liver-cysts, and which he regards as the youngest stage of the *Coccidia.* The bodies under discussion are described as about the size of a red blood corpuscle, sometimes larger or smaller, some spherical, others oval, some elliptical, others sickle-shaped, and occasionally even provided with fine processes. A distinct membrane is not visible, but a nucleus is usually quite distinct. Waldenburg believed he could observe an "apparently" active, " at any rate not wholly " passive movement, and felt warranted in regarding them as amœboid organisms.

Nor is Waldenburg the only one who maintains the further development of the four parts. Rivolta also reports similar processes, but he supposes that the parts do not segment afresh, but gradually form internally, at the expense of the granular mass, two, three, or four shining bodies, which represent the germs (" micrococchi psorospermici"). They possess great power of resistance to external influences, and can even survive desiccation. In the first reports (1869) these germs, and even the segmentation spheres, were credited with cilia, and regarded as Infusoria.

I cannot deny that really observed states lie at the foundation of these representations ; nevertheless, I cannot regard the changes which they exhibit as normal stages in the development of the parasites, but consider them simply as the phenomena of a dissolution which takes place in old infusions, as above indicated. The spores change their earlier ovoid form for a rounder one, the rod inside becomes indistinct, the shining heads become displaced and disjointed, or the whole rod may fall into pieces, while the granular mass becomes inflated, and the granules flow together into coarser grains ; a series of deceptive appearances thus originating to which the influence of a fixed idea easily lends an undue importance.

Even in Lieberkühn's researches we find figures which exhibit such

abnormal states. This is true at least of the "transparent balls," of varying number, which surround the contents or segmentation spheres,[1] which I know from my own experience to be referable only to changes which have befallen the *Coccidia* in earlier stages before the formation of the rod.

I have never been able to establish an independent exit of spores or of rods. Sometimes, indeed, I found free spores in my infusions, but so seldom, that I am inclined to think they had been liberated by mechanical influences. It is perhaps, therefore, to be concluded that the germs usually find entrance into the subsequent host while still within the *Coccidium*-shells. A transference in the free state, as maintained by Waldenburg, is very improbable, since after their arrival in the stomach they are for a time exposed to the influences of the digestive juices, which they could hardly sufficiently resist without a protective shell.[2]

We may then conclude that it is in the stomach that the rod-like germs first escape out of the shell by means of the special micropyle. Then they probably draw themselves together into a ball, become amœboid, and reach the liver by the ductus choledochus. There they bore into the epithelial cells, and become new *Coccidia.* The size of the rods suggests no difficulty, for they measure, in spite of their considerable length, hardly more than 0·006 mm. in diameter in their contracted state; they are therefore very considerably smaller than the smallest young forms I have seen (0·009 mm.). To follow out the difference between them, we may note that besides growth a certain differentiation of the protoplasm takes place, in consequence of which the parasite loses its originally hyaline nature, and becomes a purely granular nucleated mass. But these are changes which also occur in other Sporozoa in a similar manner, and may therefore be accepted without scruple. A comparison with allied organisms also corroborates the supposition that the granular mass shut in with the rod in the spore-sac is of no importance in the further development.

It is further self-evident that the conclusions here stated all require further corroboration. Our knowledge of the *Coccidia* can only become satisfactory when the processes discussed are directly observed. As long as this is wanting, we may, however, conjecture, and fill up the blanks by deductions from analogy. One must only be able to show that the suggested processes do not in any way contradict real observations.

Perhaps it may appear as though I had not myself fulfilled this condition, when I claim for the rods both contractility and mobility,

[1] "Evolution des Grégarines," *loc. cit.*, pp. 8 and 9, Tab. ii., Figs. 35 and 36.

[2] See remarks on pp. 58 and 75.

without having seen either. But the negative result is not decisive, and the less so since the conditions in which we should expect to find movement are not by any means identical with those which obtain in our incubating apparatus and infusions. But there are many parasites of whose vital energy and mobility we should form quite a false impression if we confined ourselves solely to the observation of the animal outside its host, especially if that host be a warm-blooded animal.

In support of my opinions in regard to the reproduction and development of *Coccidium oviforme*, I may finally refer to the observations which Eimer has made on the intestinal *Coccidia* of the mouse,[1] a form which cannot, however, as it is by Eimer, be directly identified with the hepatic Psorosperm.

In the intestine of the infected mice, which seemed almost synonymous with all the mice of that locality, Eimer found a great number of small sickle-shaped curved creatures of from 0·01 to 0·016 mm. in size, with a generally homogeneous shining appearance, and at most containing extremely fine granules. In size, form, and structure they were most undeniably like the transparent rods above described. Sometimes these were surrounded by a spherical, delicate membrane (0·011 mm.), which (Fig. 113, *D-F*) enclosed six or eight in an often regular arrangement; but, as a rule, they were free and isolated, and in continual motion. They bent stiffly together, and stretched themselves again, sometimes more quickly, sometimes after longer intervals, and finally, they assumed under the eye of the observer, by contracting and rolling up, the form of a clear homogeneous ball, about the size of a white blood corpuscle, and exhibiting an amœboid movement (Fig. 113, *G*). Such balls were seen in hosts in the mucus, and also inside the epithelial cells of the intestine. Besides these, still larger cells were to be seen, with nucleus and finely granular contents. They passed on the one side through a series of intermediate forms into the homogeneous balls, and, on the other hand, they might be traced through all the stages of development to the adult, round (0·018 mm.) or ovoid (0·026 mm. long, by 0·016 mm. broad) *Psorospermiæ*. The latter contain sometimes scattered, sometimes aggregated contents, as in *Coccidium oviforme*, and were, like them, provided with a smooth, double contoured shell, sometimes with a recognisable micropyle at each end. Eimer sees in these "*Psorospermiæ*" the encysted stage of a Gregarinoid parasite, which he calls *Gregarina*, in reference to the appearance of the young forms.

The dung of these mice contained, besides the usual forms of Psoro-

[1] "Ueber die ei- oder kugelförmigen sog. Psorospermien der Wirbelthiere:" Würzburg, 1870.

sperm, others, in whose granular contents were embedded varying numbers of clear shining bodies, of about the size of the smallest amœboid cells. These were found both in the cysts with diffuse contents and in those in which the contents had been retracted from the wall.

In a subsequent investigation similar stages were also found in the intestine. And further, it was proved that the shining bodies not only multiplied at the expense of the granular mass, but were also changed into sickle-shaped Gregarines, which were surrounded by a membrane originating in the outer surface of the granular ball (Fig. 113, *B*, *C*), and which issued from the Psorosperm capsule in this envelope. Already very decided movements could be observed in the young Gregarines, which pushed against one another in the most varied way within the common covering. Sometimes the movements of the isolated animals were to be seen, as above described. They manifested themselves sometimes as contractions, in consequence of which the sickle-shaped structures became "apparently rod-like bodies with terminal balls," and thus assumed a shape in which they perfectly agreed with the rod-like germs of the common *Coccidia*. Between the Gregarines there was often to be seen a spherical remnant of the original granular mass inside the enveloping vesicle.

FIG. 113.—*Coccidia* from the intestine of the domestic mouse. *A*, Inside an epithelial cell, still without capsule ; *B* and *C*, Encapsuled forms, with Psorosperms and germs ; *D-F*, Isolated Psorosperms ; *G*, Amœboid brood (after Eimer.)

There can be no doubt that the enveloping vesicle in the above case is to be regarded as a real Psorosperm, which produces a considerable number of rod-like or sickle-shaped germs, but itself originates singly within the "encapsuled Gregarine." Since the formation of spores and germs takes place, as in the so-called *Klossia* and *Benedenia* (p. 108), within the body of the host, the whole development of the parasite progresses in continuous succession,[1] and there

[1] It is a striking fact that Eimer observed in *Psorospermiæ* preserved in chromic acid solution not the above developmental process, but a peculiar segmentation of the granular contents, in consequence of which three, four, six, and probably even twelve granular balls were formed under the capsular membranes. Besides these, there also appeared on several occasions, sickle-shaped, shining structures which agreed with the young Gregarines, except in the absence of vital phenomena (*loc. cit.*, p. 15).

thus result, in spite of all other analogies, such considerable differences between *Eimeria* and *Coccidium oviforme* that an identification of the two seems quite impossible.

In view of this fact, the question presses, whether the *Coccidia* observed in the intestine of other Mammalia—the dog, cat, rabbit, and man—are not perhaps also different from *Coccidium oviforme,* found in the liver of the rabbit? Hitherto these organisms have been considered as quite identical or as but slightly different. They were all nothing else than "oval or spherical *Psorospermiæ.*" But that is of course no reason for at once regarding them as specifically identical. Even the common body-form and the similarity of the parasitism are not enough; the same might be said of *Eimeria,* but if Eimer's observations be correct, it is a separate form. It is true that such peculiarities of reproduction and development as Eimer described in *Eimeria* are not to be observed in the intestinal *Coccidia* of the other Mammals. In fact, the latter agree closely, so far as we know, with *Coccidium oviforme,* so that we have hitherto ranked them together without scruple.

But none the less does the identification of intestinal and hepatic *Coccidia* seem to me unwarranted, or even, to tell the truth, improbable.

I have previously noted the differences which obtain between them in the duration of their period of incubation—the former require hardly as many days as the others weeks. The suggested explanation of this difference has also been noticed, but this could hardly be a sufficient explanation when the two forms were regarded as identical, while, on the other hand, their divergent habit makes further discussion unnecessary. It must also be remembered that the *Coccidia* in question (both of course in their encysted stage) differ not inconsiderably in size. While the hepatic *Coccidia* are described by all investigators as bodies 0·015 mm. broad by 0·032 to 0·037 mm. long, the dimensions of the intestinal *Coccidia* in the rabbit (according to Reincke and Neumann, the only investigators who give measurements) are 0·024 mm. long by 0·0128 to 0·012 mm. broad. Thus the latter are very decidedly smaller than the former. Finally—and this fact is very important for the decision of the question—there is no case known[1] in which the two kinds of *Coccidia* have been found beside one another in the same organism,[2] although that ought surely to be very frequent, if not constant, if the same germs were able to develop either in the intestine or in the bile-ducts.

[1] In the cases of intestinal *Coccidia,* mentioned by Reincke, Waldenburg, and Klebs, the absence of hepatic *Coccidia* is expressly stated.

[2] This does not in any way contradict the possibility of the two forms occurring in the same organism, indeed this no doubt frequently occurs.

I think we may therefore, in the meantime, conclude that the intestinal *Coccidia*, which have been observed by Kjellberg[1] and Eimer[2] even in man, constitute a species different from *Coccidium oviforme*, characterised especially by their smaller size, their short period of incubation, and their position in the epithelial cells of the membrana villosa. Considering the changes in the epithelium effected by this parasite, and first observed in this case, the species may be not unfittingly named *Coccidium perforans.*

[That the intestinal *Coccidia* of Mammalia belong to numerous different species may be seen not only from the forms observed by Eimer, but also from the discovery of *Coccidium Rivoltæ*, Grassi, which inhabits the large intestine of the cat, and, after a period of cultivation in water, produces two Psorosperms, each of which yields four sickle-shaped bodies.[3]—R. L.]

Pathological significance of Coccidia.

The foregoing account shows indubitably that the changes caused by the *Coccidia* in the bile-ducts and liver are, or may be, of fatal importance. They not only exert a pathological influence by interfering with the normal function of the liver, by obstructing the secretion of bile over a more or less considerable area, by destroying the tissue of the gland, and thus restricting the quantity of secretion, and by deteriorating the quality of the latter by mixture with other substances, but also by pressing on the blood-vessels of the liver, and causing more or less intense disturbances of the circulation according to the position and size of the tumour. To what degree metabolism may be affected in consequence may be illustrated by the fact that, according to my honoured colleague Professor Cohnheim, it is impossible to produce diabetes by the usual operation in a rabbit infested with *Coccidia.* As soon as the disease has attained a considerable development, the animals die. They become very thin after being sickly for some weeks, they lose their appetite and previous activity, begin to breathe quickly and violently, and finally die in convulsions.

Nor does the rabbit alone thus suffer, but even man, although he is obviously not exposed in the same degree to the possibility of a frequent and numerous introduction of germs, is occasionally affected; and the first case which has come within the range of observation,

[1] *Virchow's Archiv f. pathol. Anat.*, Bd. xviii., p. 527, 1860.

[2] *Loc. cit.*, p. 16.

[3] See Grassi, "Intorno ad alcuni protisti endoparassitici," *Atti Soc. Ital. Nat. Sci.: Milano*, vol. xxiv., 1881.

described by Gubler in Paris,[1] furnishes us with a striking instance of what, under some circumstances, may be the result of their presence.

The case was that of a stone-breaker, forty-five years of age, who sought admission to the hospital, suffering from disordered digestion, bad appetite, sour stomach, and anæmia. He felt a dull pain in the right hypochondrium, associated with a cachectic appearance. Percussion revealed a considerable enlargement of the liver, and palpation disclosed a markedly projecting spherical tumour, lying about the position of the gall-bladder. The diagnosis referred the disease to *Echinococcus*. In the next few weeks the anæmia increased so much, that finally the lips were no longer distinguishable in colour from the rest of the face; the patient then fell one day to the ground, after which ague, and afterwards violent pains in the body, fever, feeble pulse, vomiting of bile, and collapse followed. After a night of delirium, death supervened.

A *post mortem* examination showed that the patient had died of peritonitis. In the substance of the much enlarged liver there were found about twenty tumours of cancerous appearance. Most of them were about the size of a chestnut, some even as big as an egg, and the one which had been seen from the outside was of enormous size, 12-15 cm. in diameter. Internally, the encapsuled tumours contained a thick creamy fluid of a greyish-brown colour, here and there somewhat reddish, in which there were, besides numerous altered epithelial cells and blood corpuscles, countless egg-like bodies, which, according to the figure and description, possessed all the characteristics of *Coccidia*. At the sharper end of the shell, Gubler saw a small flattening "like a lid or micropyle." In many cases the granular contents were rolled together into a ball. The wall of the tumour was strongly injected, and was at one point also ulcerated.

After the above description, I need say nothing further as to the nature and danger of the disease. The patient perished exactly in the same manner as the infected rabbit. It is not, of course, known how the infection occurred, but if one may judge from the extent and intensity of the disease, it must have been often repeated. In France rabbits are very commonly reared in hutches; and one may there-

[1] Gubler, "Tumeurs du foie déterminées par des œufs d'helminthes et comparables à des galles observées chez l'homme," *Mém. Soc. Biol.*, 1858, with illustrations, and also *Gaz. Méd.*, p. 657, 1858, Paris, or Davaine, "Traité Entoz., p. 288, 2d ed. As the quotation shows, the true nature of the affection was not recognised. Gubler regarded the *Coccidia* as eggs of *Distomum*, although he sought in vain for the worms, and was unable to decide whether the presence of these reputed eggs were only an aggravation, or the cause, of the tumours. I was the first to recognise the true nature of the parasites (see the first German edition of this work, Bd. i., pp. 49 and 740), and the importance of the case was then for the first time rightly appreciated.

fore suppose with a certain probability that the patient lived in conditions in which he was associated with the animals in such a way that the *Coccidia* voided in the rabbits' dung were transferred to him. Perhaps he had for a lengthened period drunk from a cistern standing in connection with the rabbits' hutches.

If we are not mistaken in our supposition as to the mode of transmission of the hepatic *Coccidia*, man may derive them from rabbits by eating substances which have been contaminated by their excrement; and considering the frequency with which these animals occur in our yards and houses, it is very probable that the *Coccidia* have a wider and more frequent distribution than is generally supposed, though perhaps occurring only in certain localities and in small numbers.

Nor is this a mere probability. Even in the first edition of this work I was able to report[1] that Dressler had found *Coccidia* (*Psorospermiæ*) in the liver of the human subject. They were enclosed in three cysts about the size of a millet-seed or a pea, which lay close to the periphery of the liver. The character of the contents, as seen in the accompanying reproductions of his figures, left no doubt as to the nature of the tumours (Fig. 114).

I am indebted to the courtesy of Professor Perls in Giessen for being now able to cite two additional cases: He sent me last No-

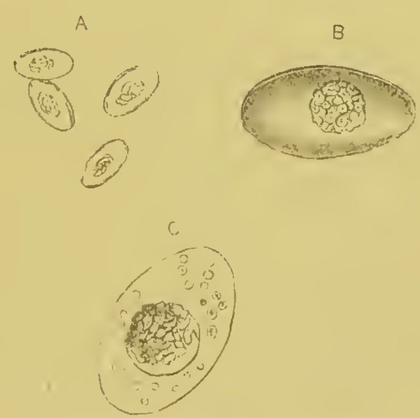


FIG. 114.—*Coccidia* from the human liver—*A* × 330, *B* and *C* × 1000.

vember a drawing and a section which had been made by Professor Sattler in Vienna during a course of pathological anatomy. From both drawing and preparation one could recognise the cross-section of an enlarged bile-duct, with a very proliferous epithelium and with *Coccidia*. The latter were partly removed from their original position

[1] *Loc. cit.*, p. 740.

and scattered in groups, so that they looked as if embedded in the surrounding connective tissue. Since the contents of the *Coccidia* were quite clear, as is always the case in preparations mounted in glycerine, the bodies might easily have been mistaken for eggs of *Distomum* (*D. lanceolatum*), but in my further examination any doubt as to their true nature was wholly removed.

The other case was based on a preparation from v. Sömmering's collection annexed to the Pathological Institute in Giessen. It showed ulceration of the bile-ducts, in which *Coccidia* were to be seen. The label bore the words, "*An Distomis orta*," which perhaps originally read "*Distomatis ova*."

But it is not only the liver, but also the intestinal canal, which is invaded by these parasites, and to a greater or less extent affected by them. We know cases, apart in the meantime from man, where not only rabbits, dogs, and cats, but also other mammals—sheep, pigs, guinea-pigs, and moles—were infested with these intestinal *Coccidia*. Those of the mouse and others belong, as we have noted, to a distinct species. The same is true of the *Psorospermiæ* of fowls,[1] ducks, and geese, which, according to a preparation kindly lent me by Professor Zürn, differ from mammalian *Coccidia* in their spherical form, in the thinness of of their shell, and in their smaller size (0·002 mm. in diameter), but agree with them (according to Rivolta) in their life-history. I have myself only studied the intestinal *Coccidia* of the dog and the cat. In the case of the latter, I could most distinctly convince myself that the *Coccidia* were contained in the epithelial cells until perfectly ripe. This is much more easily demonstrated than in the case of the hepatic *Coccidia*, for the intestinal epithelial cells, perhaps because of their opercular structure, have a greater permanency of form, and remain closed even when abundantly infected.

In the milder cases the *Coccidia* are sometimes scattered, sometimes arranged in groups. In the latter case one can recognise the infected places even with the naked eye as somewhat elevated whitish spots of varying size. There are also cases in which the surface of the intestine is uniformly infected and considerably swollen, so that it looks as though it were overlaid with a false membrane. I found it thus, particularly in a dog which had served for an experiment with *Trichina*.[2] The parasites are usually most crowded in the villi, which then appear like little white points, as after an absorption of chyle, so that it has even been conjectured that the *Coccidia*—of course, as normal structures—might play some part in the absorption of fat.[3] The

[1] The occurrence of *Psorospermiæ* in birds was first observed by Rivolta (1869).

[2] In another dog infected with *Trichina* I found numerous *Coccidia* in the intestine: Virchow has also made the same observation.

[3] Finck, "Sur la physiologie de l'epithelium intestinale," Thèse Strassbourg, p. 17, 1854.

Lieberkühnian glands are not unfrequently filled with them, and sometimes swollen out to double their normal diameter.[1] The surrounding tissue is then infiltrated and inflamed, and sometimes degenerates in small but distinct ulcers. To all appearance this is especially common in rabbits, where (according to Reincke) the glands of the cæcum and of the vermiform appendix very frequently undergo similar alteration.[2]

It is obvious that the changes wrought by these intestinal *Coccidia* —destruction of the epithelium, swelling, and inflammation of the sub-mucosa, ulceration, &c.—cannot be without derangement of function, and in this connection numerous differences in the extent and intensity of the disease will be observed. Dyspepsia, loss of appetite, imperfect nutrition, colic, looseness of the bowels, are the most constant attendant symptoms.[3] In rabbits and mice these are often so aggravated that death ensues.

As to the phenomena caused by the parasitism of *Coccidia* in man, nothing really is known, since few instances only have yet been observed. With the exception of Kjellberg and Virchow,[4] Eimer is the only one who mentions the subject. He reports[5] how, in the Pathological Institute at Berlin, he had twice seen bodies in which the intestine was "filled" with *Psorospermiæ* similar to those occurring in animals. "In both cases the epithelium of the intestine was for the most part destroyed and riddled by the Psorosperms," just as Eimer had also observed in mice which had died of Gregarinosis.[6] Unfortunately, neither a history of the illness nor an authentic report on the *post mortem* examination could be procured; and only this was ascertained, that one of the two men had belonged to the ward for the insane.

As regards the infection, what I have said of the hepatic *Coccidia* must hold good here, with this alteration, that it might be brought about by dogs and cats as well as by rabbits.

[1] Lieberkühn erroneously regarded these glands filled with *Coccidia* as Psorosperm-tubes, and therefore, with apparent justice, identified the *Coccidia* as true Psorosperms.—"Evolution des Grégarines," *loc. cit.*, p. 29.

[2] Reincke reports finding the young stages of these parasites even in the mesenteric glands:—"In glandulis mesentericis et in mesenterio secundum vasorum tractum noduli subflavi inveniebantur, quos psorospermia priorum evolutionis graduum impleverant." *Loc. cit.*, p. 1.

[3] Rivolta found the "*Cellule oviforme*" frequently in the intestinal villi of dogs which had been killed on suspicion of madness—"Studi fatti nel cabinetto di anatom. pathol. di Pisa," p. 42, 1877. I have, however, doubts whether this were a case of true *Coccidia*.

[4] *Virchow's Archiv f. pathol. Anat.*, Bd. xviii., p. 523, 18 .

[5] *Loc. cit.*, p. 16.

[6] "In many parts the intestine contained scarcely anything but epithelial cells, "Psorosperms," or cells, and when these had fallen out from the hardened cross-sections of the intestine, I saw that the wall looked as if small holes had been punched in it, or as if it had been eaten through."—Eimer, *loc. cit.*, p. 13.

Lindemann reports[1] having found Psorosperms even in the human kidney, in the case of a patient who died of Bright's disease in the hospital at Nijni Novgorod. The parasites appeared to the naked eye as small brownish-black masses, up to 2 mm. in size, which were embedded in great numbers in the tunica serosa, but covered by a thin layer of the same. "In my microscopic examination," Lindemann writes, "these masses were seen to be colonies of Psorosperm-balls, which were embedded in layers in the connective tissue, and surrounded by the fibrous bands which had been bent out of their course by the balls. The cells and fibres of the connective tissue were normal, excepting the bending of the fibres and the spaces thus created, in which the Psorosperms lay. Besides this, the organ was infiltrated with a mucous exudation, which contained the well-known mucous balls of Hassall" (Fig. 115).

FIG. 115.—*Psorospermiæ* (?) from the connective tissue of the human kidney. (× 320, after Lindemann.)
a. Connective tissue fibrils.
b. Connective tissue corpuscles.
c. Pseudonavicellæ, lying free.
d. Hassall's mucous balls.
A. Psorosperm-balls.

In this report one looks in vain for any sure foundation for Lindemann's identification of these structures with Psorosperms. Since this is not forthcoming, we have only the authority of the investigator to rest upon, and this has unfortunately been so much shaken by some of his later investigations,[2] that I am very doubtful whether Lindemann was right in regarding the observed structures as Psorosperm-capsules.

Still less can I recognise the "colonies of Psorosperm-balls" (Fig. 116) which Lindemann found on human hair, and I very much regret that the observations on this point were first recorded in my work, and to some extent with my guarantee. Not that I deny the presence of these structures, for they have often been observed before and since; I am only opposed to their identification with Psorosperms, and the fanciful history which was afterwards accorded to them.[3] For it was

[1] See the first edition of this work, Bd. i., p. 943, for notice of Lindemann's communication to me on the subject. Virchow has also found Psorosperms in the kidneys of the bat (*Virchow's Archiv f. pathol. Anat.*, Bd. xviii., p. 527, 1860).

[2] I will only refer to the entirely false representation which Lindemann gave of the organisation of *Echinorhynchus* (*Bull. Soc. impér. nat. Moscou*, p. 184 *et seq.*, 1865), and to my critique (*Archiv f. Naturgesch.*, Jahrg. xxxii., Bd. ii., p. 152, 1866).

[3] See Lindemann's statements, *Bull. Soc. impér. nat. Moscou*, p. 425 *et seq.*, 1863, and specially p. 282, 1865.

not simply moving Gregarines from which the structures seated on the hair were produced by encystation and spore formation,[1] but

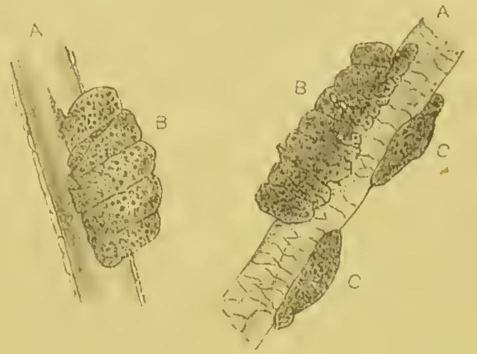


FIG. 116.—Lindemann's Psorosperm-balls (*B*) and Gregarines (*C*) on human hair.

Gregarines which were transferred to the hair from the intestine of the louse, and which had Psorosperms of such power of resistance that even the coiffures of ladies were infected with potentially active germs, from which these Gregarinoid creatures escaped, and, wandering into the body of their host, became again Psorosperms in the most varied organs, and gave rise to manifold troubles.

Although coiffures have been absolved from all complicity in the production of "Gregarinosis," it is nevertheless quite possible that our experience as to the pathological nature of the Psorosperms is not yet by any means complete. Thus Zürn has lately come to the conviction that the infectious virulent influenza of the rabbit—an often fatal rhinitis, which usually spreads rapidly from the nose to the pharynx and tympanum, and, after perforation of the membrane, sometimes attacks the external ear or passes to the intestine—is caused by parasites,[2] which can be observed in great numbers as naked Gregarines and *Psorospermiæ* in the affected mucous membranes and their secretions. Similarly Silvestrini and Rivolta were able in 1872 to refer an epidemic prevalent among the fowls around Pisa to Psorosperms.[3] The disease was localised, like the influenza of the rabbit, in the pharynx, larynx, and nose, but sometimes affected the conjunctiva, intestine, or even the comb. The observers saw that

[1] Knoch, who investigated Lindemann's hair Psorosperms in Russia, certainly had the same structures under observation, but never found mobile forms (*Journal des russischen Kriegsdepartements*, Bd. xcv., 1866).

[2] "Die kugel- und eiförmigen Psorospermien als Ursache von Krankheiten bei Hausthieren," p. 14, Leipsig, 1878. The infectious catarrh of rabbits is described as a fungoid disease in Von Schmidt's work, "Die mycotischen Erkrankungen der Respirationsorgane, speciell der Kaninchen:" Hofgeismar, 1877.

[3] *Giornale di anatomia, fisiologia e pathologia degli animali*, Pisa, 1873; see also Rivolta, "Parass. veget.," p. 390.

the epithelial cells (in the comb, the epidermal cells, as far as the Malpighian layer) were penetrated and altered by *Coccidia*, and that the subjacent tissue was swollen and inflamed, so that the animals were for the most part starved or suffocated. The nature of the disease was placed beyond all doubt, not only by observation, but also by experiment, of which, however, the constant result was that, as before mentioned, only the *Coccidia* with segmented contents caused infection, while the younger stages traversed the intestine passive and harmless.

In conclusion, I must once more repeat that the true *Coccidia* do not include all the forms which investigators of the higher animals have considered *Psorospermiæ* and designated as such. Among the latter I would, for instance, class the "green" *Psorospermiæ*,[1] which Paulicki describes in apes, and which were found in the lungs both of adult and of newly born animals. Their chlorophyll contents are sufficient to exclude them from the *Coccidia*.

Class III.—INFUSORIA.

Ehrenberg, "Die Infusionsthierchen als vollkommene Organismen:" Leipzig, 1838.
Dujardin, "Histoire naturelle des Infusoires :" Paris, 1841.
Claparède et Lachmann, "Études sur les Infusoires," Parts i. et ii.: Génève, 1858-61.
Stein, "Der Organismus der Infusorien," Th. i.-iii. : Leipzig, 1867-1878.
Bütschli, "Ueber die Conjugation der Infusorien," *in* "Studien über die ersten Entwickelungsvorgänge der Eizelle, die Zelltheilung, und die Conjugation der Infusorien :" Frankfurt, 1876.

Protozoa with a more or less definite body-form, and provided with cilia, which are placed on the body in varying number and arrangement. The protoplasm, especially of the higher forms, is differentiated into an outer layer and a central mass, which sometimes encloses a single nucleus, sometimes more, and very generally one or more contractile vacuoles. With the exception of some parasitic species, all of them have a mouth, or one or more mouth-like openings, serving for the ingestion of food, and most of them have also an anus.

The name "Infusoria," which has been a familiar word for more than a hundred years, is used to denote those organisms discovered by Leeuwenhoek, which are constantly found in organic infusions, in which indeed they were thought to be spontaneously generated. This is not, however, their proper or normal habitat, which is rather to be sought in stagnant or sluggish water, while its countless microscopic contents furnish a rich supply of nourishment to these minute

[1] "Beiträge zur pathol. Anat.," p. 61, 1872.

organisms. In the economy of Nature this fact is of pre-eminent importance, for by the invisibly active life of these organisms a large quantity of organic substance, which would otherwise be lost to the animal world, is appropriated and utilised, and the more fully inasmuch as in wealth of form the Infusoria are second to no other group, and in number of individuals largely exceed all others. The latter statement is specially true of the putrefactive Infusoria, for these are found along with fungi and Schizomycetes, in a truly astounding multitude, wherever there is any abundant putrefying substance in the water. It is therefore not surprising to learn that numerous forms have found a fit environment in the intestine, and especially in the rectum of living animals.

The Infusoria are most conspicuously separated from other Protozoa by the possession of cilia and an oral aperture, two structures in this case naturally associated together since the body has not only a more or less firm cuticle which prevents the formation of pseudopodia and amœboid ingestion, but has also very generally a firmer cortical layer, which encloses the less dense protoplasm and the abundant remains of food.

By means of their cilia, the Infusoria have the power of swimming somewhat rapidly, though there are species which, after a longer or shorter free life, become attached to some foreign object. Some of these—the so-called *Acinctæ*—even lose their cilia after becoming fixed, so that their true nature is easily overlooked, especially since, instead of a mouth, they have a large number of openings mounted on long thin tubular stalks, which enable their bearers to catch and suck the juices of other small animals, mostly Infusoria.

In this world of invisible life, moreover, these predaceous forms lead on to others, which are parasitic. Besides the free *Acinctæ*, there are also other Suctoria, which, instead of killing their prey—usually larger ciliated Infusoria—only bore their way into them, and live there as parasites. They grow at the expense of their host, and by repeated division produce a numerous progeny, which, on reaching maturity, break through the body-wall, swim about for some time by means of their cilia, and finally return again to an Infusorian host.[1]

The *Cilia* exhibit such great and characteristic differences in number and arrangement, that these have been used, not without good results, for systematic purposes. Sometimes the whole surface of the body, sometimes only certain parts, are provided with cilia, and their

[1] These parasitic forms have attained a somewhat unhappy prominence in the history of our knowledge of the Infusoria, since they have given rise to the idea that the ciliated Infusorians were viviparous, and produced "*Acincta*-like embryos" (Stein). The parasitic nature of these so-called embryos has, however, been experimentally established; see Bütschli, *Zeitschr. f. wiss. Zool.*, Bd. xxv., p. 426, 1875.

number is in the latter case generally small. In a large and rich group—the Flagellata—there is usually only a single flagellum, or at most but a few.

It is especially the region round the mouth which in such cases bears the cilia, and this is intelligible when we remember that the cilia act not only as locomotor organs, but also in capturing the food. A little whirlpool is set up by their movements, and the minute bodies suspended in the water are swept into the mouth. For this purpose the oral cilia often have a special arrangement, and a more vigorous development than those on other parts of the body.

The food, which usually consists of fine granules, becomes agglomerated into a round ball at the lower part of the mouth, and this is swallowed only when it has attained a certain size. It is of course the adjacent parts of the contractile cortical layer which effect this swallowing, and transfer the morsel through a sort of gullet (of course without special walls, and really only a slit in the parenchyma) into the central substance. Some specimens living in favourable nutritive conditions often have their central substance filled with numerous balls of food. Organic pigments, such as carmine and indigo, are similarly ingested, and were first described in 1777 by Baron von Russworm-Gleichen in a work on microscopic objects.[1] The food-balls, under the pressure of the surrounding body-substance, glide inwards in more or less regular courses, and here and there coming in contact, they flow together; and one can follow step by step the various changes which they undergo under the action of the juices mixed up with them, until finally the remnants are expelled by the anus. This lies usually at the posterior end of the body, opposite the mouth, though there are instances in which the anus is near the oral end, and in which the mouth is displaced, and comes to open near the middle of the body.

When the food does not consist of fine granules, as is the case in some Infusoria, but of larger bodies (plants and animals), the mouth is usually a very wide and extensible cleft, which extends over a considerable proportion of the whole body.

An *Alimentary Canal* is never present; nor are the numerous "stomachs" described by Ehrenberg (hence the name "Polygastrica") anything more than the food enclosed in vacuoles of the body-substance. What has been previously said of the Rhizopoda holds true of the Infusoria, which only differ in the persistence of the openings for ingestion and expulsion; and we have already mentioned that these openings are sometimes wanting. So far as we know, however, this occurs only in certain parasitic forms (species of the genus *Opalina*), which, living continually surrounded by fluid nutriment, require only

[1] "Mikroskopische Augen- und Gemuthsergötzungen," 1777.

power of absorption through the outer membrane. It is extremely improbable that this mode of nutrition occurs in any free-living form, although it is often so alleged. Albuminoid solutions soon putrefy, and never occur around living organisims in a state which would ensure all the properties essential for the nutrition of an animal; so that if they feed by imbibition, it must be on inorganic substance; in other words, they must be referred to the vegetable kingdom. A free-living animal requires the power of incorporating a firm (*i.e.*, resisting) organic substance, and therefore, when a cuticle and cortical layer are present, it requires a mouth.

The *Cortical Layer* is, as we have indicated, the special seat of the animal functions. This is proved not only by direct observation, but by the fact that in the larger forms a striation is sometimes seen resulting from a layer of fibrils. This occurs, for example, in the stalk of the familiar bell-animalcule (*Vorticella*), and presents a distinctly muscular appearance. The course of the fibrils always corresponds with the direction in which the contraction takes place, and is predominantly longitudinal.

To this cortical layer belong the vacuoles, which, in the Infusoria, usually occur at distinct places, and which, by their more or less frequently repeated rhythmic contractions, convey the impression of hearts. The resemblance is further increased when sometimes special lacunæ are found in connection with the pulsating space, as vessels with the heart. These are especially visible at the moment of systole, when the fluid contained in them is in a state of tension, and their observation is as easy as it is beautiful, *e.g.*, in the common slipper-animalcule (*Paramœcium aurelia*). After contraction the fluid often collects in little isolated drops, which afterwards flow together into a larger vacuole. This is a certain proof that the vacuoles have no independent surrounding membrane, but owe their contractility solely to the surrounding cortical layer. Their contractility varies considerably in different species, being sometimes rapid and frequent, and in other cases slow and at long intervals. Even in the same individual differences are observable at different times and states; but this may at least be said, that in general the liveliness of the pulsations is proportionate to the general energy of the animal and the temperature of the surrounding medium.

Our decision as to the functional import of this apparatus depends very essentially on the fact that in several cases it has been most distinctly proved that it communicates with the exterior by an opening, sometimes temporary, sometimes permanent, and rarely by the anus.[1] Thus the contractile vacuole of the Infusoria so closely

[1] See especially Wrzésniowski, *Archiv f. mikrosk. Anat.*, Bd. v., p. 25, 1869.

resembles the excretory apparatus of the flat-worms, that we need hardly scruple to claim for it a similar excretory function, and regard it as expelling the superfluous water and the waste products of metabolism.

The *Nuclei*, as well as the contractile vacuoles, lie in the cortical layer. This is especially the case with the nucleus *par excellence*, which is seen usually, even on superficial observation, and still better after the use of acetic acid, as a conspicuous, firm body, sometimes showing a division into two or more parts of round, elongated, or occasionally ribbon or garland-like form, and whose resemblance to a ordinary cell-nucleus first suggested the idea that the Infusoria were unicellular organisms. But even von Siebold found besides this nucleus, and generally closely adjacent to it, the so-called "nucleolus"—a sharply defined, minute, shining body—more than one sometimes being present, although it has not been demonstrated in by any means all the species.

Both bodies are not only of high importance in determining the morphology of the Infusoria, but have been the subject of much discussion and study during the gradual development of our knowledge of the reproductive process in the Infusoria. For a while the opinion seemed plausible that these two structures represented the sexual organs. This theory was especially based on the observations and conclusions of Balbiani,[1] and was very generally accepted,[2] especially as it seemed in a satisfactory way to sum up a series of more or less unco-ordinated results.

According to the theory supported by Balbiani, the nucleolus is the male reproductive gland in its undeveloped state, and the nucleus, which Ehrenberg had previously called the "testis," is, indeed, the ovary.[3] Appearances are certainly in favour of such a theory. One sees the nucleolus swell up under certain circumstances, and become a long vesicle, whose contents gradually assume a striated appearance, as if they were a bundle of spermatozoa.[4] While the nueleolus undergoes these changes, and finally divides into a number of balls, resembling sperm-capsules, the nucleus, which is meanwhile much enlarged, also falls asunder into a number of round masses, which

[1] "Recherches sur les phénomènes sexuels chez les Infusoires," *Journal de physiologie*, t. iv., 1862.

[2] The account given of the sexual reproduction of the Infusoria in the first edition of this work owed its origin to the influence of this theory.

[3] According to Ehrenberg, the sperms gained the exterior by means of the "contractile bladder," which thus became a sort of seminal vesicle.

[4] Joh. Müller, Lieberkühn, and Claparède and Lachmann had remarked this appearance before Balbiani, and had noted the likeness between the threads and spermatozoa, without, however, identifying the two.

might well be regarded as ova, and which Balbiani, indeed, credited with all the properties of such structures.

According to Stein, who in general supported this theory, the eggs develop inside the maternal body, and the resulting embryos, for which he mistook the above-mentioned parasitic Suctoria, leave the mother in the form of *Acinetæ*. On the other hand, Balbiani alleged that he had repeatedly observed the laying of these "eggs," and he therefore regarded the Infusoria as oviparous animals.

What still further increased the resemblance between these processes, thus shortly summarised, and the phenomena of sexual reproduction, was the fact that they were preceded by a veritable copulation.

Even Leeuwenhoek believed that he had seen his Infusoria in the act of pairing. Other investigators, like Russworm-Gleichen and O. F. Müller, asserted the same thing, but their results fell into discredit, and were forgotten, when Ehrenberg and Dujardin explained the phenomenon as a peculiar case of the longitudinal division which they had so frequently demonstrated among the Infusoria. At any-rate, the credit is due to Balbiani of having recognised that the conjugation of two originally distinct individuals was an actual fact. In this act the two animals lie together with their mouths in contact, not only superficially, as Balbiani would have it, but so intimately that the connecting parts are sometimes absorbed, and the animals form a double body for several days. Balbiani interpreted this as an act of copulation, in which the sperms were mutually exchanged. Stein[1] also recognised a distinct association between the copulation and the reproduction of Infusoria, but refused to regard the act as an actual fecundation. He considered it as analogous to the conjugation of certain lower plants—a process which seems to bring to maturity the hitherto inactive and undeveloped sexual organs, or so to change them that a subsequent (self) fertilisation[2] becomes possible. He supports this opinion by observations, according to which the sperms became ripe as a rule, only after the separation of the conjugating individuals—a fact in direct antagonism to the theory of actual copulation. He further cites cases in which the conjugation ("Syzygie," Stein) leads to a complete and inseparable union of the two individuals.

These relations began to assume a somewhat changed complexion in the light of the facts advanced by Bütschli, which excluded any comparison with the processes of sexual reproduction, and furnished new

[1] At least in the second volume of the researches above referred to.

[2] It is striking that Stein speaks only of a fertilisation of the nucleus of the embryonal sphere, which performs the functions of an ovary, and not of the egg-like bodies which result from this by segmentation.

and very cogent reasons for the comparison of the Infusorian body with a cell. The investigations of this excellent observer prove that changes of the nucleolus, quite similar to those above described, may often be observed in the nuclei of ordinary dividing cells and segmentation masses. The ordinary supposition that in division the nucleus of the cell simply separates into two parts was shown to be a mistake, due partly to the variable and often unfavourable condition of the material examined, but much more to the minuteness of the object and the use of insufficient microscopic power. In reality the process is a complicated one, accompanied by a transformation of the contents, which essentially resembles the formation of nuclear fibres in the Infusoria. After this phenomenon was once recognised, it was repeatedly observed with various modifications in the most diverse kinds of cells (also by Strasburger in vegetable cells), and was in fact proved indubitably to be of general occurrence. The apparent "sperm-balls" were therefore divided nuclei, which afterwards reassume a homogeneous nature, and the so-called "sperms" were anything but what Balbiani and Stein[1] had supposed.

The *Nucleolus* of the Infusoria is thus a structure which, in its essential morphology, coincides with the nucleus of the ordinary cell, and may therefore be justly identified with it. It is not, then, sexual maturity which finds expression in its transformation, but simply the commencement of division, which, as a matter of fact, follows close upon the process of conjugation. This mode of multiplication is not, however, confined to the time immediately following conjugation. It also occurs later, but happens most frequently and constantly in those forms which have previously conjugated. So far as we know, this process and its modifications (including budding) is the only mode of reproduction exhibited by the Infusoria.

But if, as we have maintained, the "nucleolus" represents the nucleus of the Infusorian body, what, then, is the "nucleus" to which this position is usually accorded? Again the process of conjugation sheds light on the question. The observations on this point, especially of Bütschli, inform us of the surprising fact that the portions of the "nucleus" are indeed, as Balbiani affirmed of his "eggs," generally expelled during conjugation, without, indeed, ever forming new individuals. Instead of this expelled "nucleus," another is formed, and that from one of the newly originated "nucleoli." Sometimes the portions of the "nucleus" are not wholly expelled, and then the new "nucleus" results from a fusion of the remainder with a "nucleolus."

[1] To establish the theory of these investigators it would have been necessary to prove that the sperms resulted from cells. But no one had tried to discover a cellular structure in the nucleolus.

There can be no doubt that both "nucleus" and "nucleolus" have the function of a cell-nucleus. The Infusorian is, in other words, provided with two quite different nuclei (a "principal nucleus" and an "accessory nucleus"), both of which undergo at certain times (during conjugation) a fundamental transformation and renewal.

That the "nucleus" is really of the nature of a true cell-nucleus is proved by the fact that under certain circumstances it also exhibits the same changes as we have previously described in the case of the "nucleolus." We know especially of some Infusoria in which conjugation has not yet been observed (*Spirochona, Podophrya, Dendrocometes*). Here it is not the "nucleolus" but the "nucleus" which assumes a fibrillated character before division, and afterwards (in its parts) reassumes its former state. Similarly, the later divisions in Infusoria take place without change in the "nucleolus." It is only the "nucleus" which participates in these processes, and falls (whether with antecedent striation or not is still uncertain) into two equal parts, one for each of the twin parts.

The above observations sufficiently prove that conjugation is of some consequence in the reproductive processes of the Infusoria. It is, however, no sexual copulation; it can hardly be said to be anything but a fertilisation,[1] as we have already hinted. At any rate, the act is no concurrence of sexual products, but of living individuals—of individuals, however, which, like the sexual products, are morphologically equivalent to cells, and as such represent in one the various organs, tissues, and also sperms and ova of the higher animals. We are confirmed in this opinion by the fact that there are Infusoria (*Vorticellæ*) in which conjugation never or seldom occurs between individuals of equal size and similar form, but between a large fixed animal and a much smaller young form, which originates in consequence of a rapidly repeated division, and stands in exactly the same relation to the fixed form that the microgonidium bears to the macrogonidium in certain Algæ—a relation which, in the case of the latter, had for long been justly regarded by botanists as equivalent to fertilisation.

Conjugation is further of great importance in connection with the Infusoria since the subsequent divisions occur much more frequently than would otherwise be the case. It therefore obviously serves, like genuine fertilisation, for "freshening the blood." It marks, to some extent, the beginning of a reproductive period, during which multi-

[1] This being the case, we may note the great interest attached to the resemblance between the fate of the nucleus in conjugating individuals and the changes of the germinal vesicle which accompany impregnation, especially as described in the recent researches of Hertwig, Fol, Bütschli, and others..—[See Geddes, article "Reproduction," "Encycl. Brit.," Edinburgh, 1885.—W. E. H.]

plication takes place exclusively by division, until exhaustion renders another conjugation imperative.

Fission in the majority of Infusoria is transverse, so that the anterior part has to form a new anus, and the posterior part a new mouth and the associated circlet of cilia. In other cases the division is longitudinal, and it may even take place diagonally. Nor is it by any means necessary that the two parts should be equal; indeed, the one is often so very minute that it looks like a little bud. When the division is repeated in quick succession, the resulting organisms are of extraordinary minuteness, which is particularly seen in the fixed forms as long as the progeny remain connected together in a group.

In many species the division only takes place after the mother-animal has drawn itself together into a ball and donned a capsule. Sometimes two, sometimes four, six, or eight young Infusoria result, which remain within the capsule till they break through it, and continue their life outside.

This encystation occurs for other purposes than that of reproduction. At other times also the Infusoria have the power of secreting a cyst and passing into a quiescent state. This may be observed on approaching scarcity of water, or when the environment is in some way abnormal. It takes place indifferently in adult and young forms. Protected by this cyst, which is often thick and very resisting, these very delicate creatures can survive complete dessication. They may be kept, like seeds or eggs of worms, for years, and yet, on the application of water, often recover their full vital energy within a few hours, and break through the capsule. The importance of this for the Infusoria is very obvious. It is not only a means of preservation, but of propagation; for the wind, passing over the dried up ditches, lifts the capsules and carries them to great distances, dropping them again in most varied situations—on leaves, moss, and bark, in chinks, bowls, and infusions. Such germs have been repeatedly demonstrated by Ehrenberg and others in atmospheric dust, by passing the air through pure water. We do not require to point out how this habit is specially favourable to the parasitic occurrence of these animals.

If the Infusoria be carried to, or in any way reach, a situation and environment which fulfil the conditions of their life, they multiply so rapidly that their number increases in a short time to an almost incredible degree. Theoretical calculations which have been made give results on this matter not less astounding than those above quoted for the Schizomycetes.

In reference to the manifold and fundamental differences between the various forms of Infusoria, we may note that the group is generally divided into "Flagellata" with a flagellum, and "Ciliata" with cilia.

The latter are at once most numerous, most highly developed, and most manifestly animals, while the Flagellates recall in many ways certain vegetable organisms, and often approach the unicellular Algæ so closely in structure and life-history, that a separation can only be based on the decidedly animal mode of their nutrition. Many Flagellata also resemble very closely the swarm-spores of certain Rhizopoda.

Both groups include numerous parasitic forms, which infest both the lower and higher animals, including man.

Order I.—Flagellata.

[Davaine, Art. "Monadiens," "Dict. sci. méd.," 1874.—R. L.]

Stein, "Organismus der Infusionsthiere," Abth. iii., 1878.

Bütschli, "Beiträge zur Kenntniss der Flagellaten," *Zeitschr. f. wiss. Zool.*, Bd. xxx., pp. 205 *et seq.*, 1878.

Dallinger and Drysdale, "Researches on the Life-history of the Monads," *Monthly Micr. Journ.*, vols. x.-xiii., *loc. div.*, 1873 to 1876.

[Grassi, "Intorno ad alcuni protisti Endoparassitici," *Atti Soc. Ital. sci. natur.*, vol. xxiv., p. 47, 1882.—R. L.]

Infusoria of small size, and with but slight differentiation of the body-parenchyma, so that the cortical layer and central mass are only faintly contrasted, and a nucleolus can only rarely be distinguished. The cilia are always confined to the anterior oral extremity, and are present either singly or in small numbers. Sometimes there is also a ciliated fringe surrounding the mouth like a collar, or running down the body in the form of a longitudinal band. An anus seems always to be wanting.

Fig. 117.—*Cercomonas muscæ* at different stages. (After Stein.)

Fig. 118.—*Bodo saltans.* (After Stein.) On the right an instance of division.

Of the numerous and often very wonderful and elegant forms of flagellate Infusorians, we are here specially interested only in those

which belong to the family Monadinæ. These creatures are, as their name suggests, almost at the extreme limit of visible organisms; they are extremely small and transparent, and have generally very few, but long, cilia (Figs. 117, 118), which sometimes propel the body rapidly about, and sometimes merely vibrate to and fro. A slight amœboid movement is also occasionally to be observed. Almost all these Infusoria live on putrefying substances, and are often found in countless numbers in water, or in living animals, especially in the rectum. The species most familiar to us are those always present in myriads in the large intestine of frogs and toads. In warm-blooded animals the Monadinæ are also among the most frequent of parasites. It is, for instance, impossible to examine any ruminant or pig without finding these creatures in countless numbers, along with other infusorial parasites, in the paunch of the former, and in the cæcum of the latter.[1] In order to observe them, it is of course necessary that the examination should take place as soon as possible after death, since they soon perish, and are then scarcely distinguishable from other small bodies. Their occurrence in man, although not exactly rare, appears to be always due to special circumstances, but when they occur it is usually in great abundance. Their presence would also be much more frequently ascertained if the evacuations could be immediately examined, or even if it were possible always to use a warm stage. By this means it is possible to keep the parasites alive for many hours, and to observe them in lively motion, if only care be taken that the preparation does not dry up.[2] Slightly acidified water appears to be the best means of moistening them, and is even capable of reviving their flagging motion. Temperatures above 50° C. and below 14° C. prove fatal, and thus the fact is explained that parasites occurring in winter die in a few minutes, especially if a cold glass slide be used. Further, as these creatures are very sensitive to solution of corrosive sublimate, and perish immediately when exposed to it, even when extremely dilute, this drug would probably furnish a very efficient remedy for them.

The parasitism of the Monadinæ is, however, by no means confined exclusively to the Vertebrata. In the genital canals of the snail, in the body-cavity of the Rotifera, and in the alimentary canal of millepedes and insects they are not at all uncommon, and occasionally are

[1] Gruby and Delafond have also observed Monadinæ in the stomach of the dog (*Comptes rendus*, t. xvii., p. 1304, 1843), and Davaine in the alimentary canal of the guinea-pig, of the hen, and of the duck (*loc. cit.*). [Grassi has recently described similar forms in the guinea-pig, mouse, and duck (*loc. cit.*).—R. L.]

[2] [Grassi (*loc. cit.*) refers the rapid death of the parasitic Monads, not so much to the fall in temperature, as to the rapid formation of acids in the evacuated fæces. Where this is prevented, the Monads may remain alive for many days.—R. L.]

even so frequent (especially in moths and flies) that whole tracts of the intestine are filled with them.

Reproduction is effected by division, which generally takes place longitudinally, and is often so rapidly repeated that the young ones remain for a time grouped close together. Dallinger and Drysdale have also observed conjugation in the Monadinæ. This is followed by an encystation, in which the contents break up, and become moveable germs, or countless, immeasurably small spores, which afterwards become new Monadinæ, and even at high temperatures (above 100° C.) do not lose their power of further development. In individual cases other

FIG. 119.—*Trichomonas batrachorum.* (After Stein.)

observers have also noted a quiescent state, which leads to the production of countless little swarm-spores.[1]

The flagella, which vary very much in number and arrangement, furnish us with the best standpoint from which to consider the individual characteristics of the various genera. But since a very strong magnifying power is necessary to establish the exact nature of these conditions, many mistakes have been made, which have been specially disastrous in the identification of the species occurring in man. The latter belong, so far as we accurately know them, to two very widely distributed genera,—*Cercomonas* and *Trichomonas*. The former of

[1] [Recently the independence of the Monads (at least of the parasitic forms) has been several times questioned, and the attempt has been made to regard them as swarming conditions of *Amœbæ*, especially in Cunningham's paper (*Quart. Journ. Micr. Sci.*, N.S., vol. xxi., p. 234, 1881). The Cercomonads are said, after encapsulation, to become *Amœbæ*, which fuse together in large numbers after losing their power of movement, and form considerable masses or even true sporangia. — R. L.]

these contains numerous free-living species, while the latter is wholly parasitic (in both higher and lower animals). The figures above (Fig. 117) represent *Cercomonas muscæ*, a parasite often found in abundance in the chylific stomach of the house-fly, and also (Fig. 119) *Trichomonas batrachorum* from the cloaca of the frog. They show

Fig. 120.—*Hexamita intestinalis*, in the young and adult states. (After Stein.)

very distinctly the differences between the species in question, yet even lately they have been more than once confounded. Along with *T. batrachorum*, and hardly distinguishable from it with a low power, there very often occurs another parasite, belonging to the genus *Hexamita*, which I also figure for purposes of comparison (Fig. 120).

Cercomonas, Dujardin.

Bodo, Ehrenberg, and others.

Monadinæ, with an oval or longish body, which is generally narrowed posteriorly, and often prolonged into a terminal filament; while anteriorly it is provided with a long and thin simple flagellum.

Cercomonas differs from the related genera, *Monas* and *Bodo* (*sensu stricto*), chiefly in the simplicity of its ciliary apparatus. At the base of the flagellum *Monas* has two short and fine hairs, which

[1] Grassi, *loc. cit.*, pp. 12-22.

are always in motion, while *Bodo* (Fig. 118) is provided with a second long flagellum, which is of a more rigid nature, and is generally directed backwards.

Each of these three genera contains forms which are said to occur in man. So at least we learn from Steinberg's microscopic researches on the white substances often found between human teeth.[1] For, besides various *Vibriones* and the above-mentioned *Amœba buccalis*, he found no fewer than nine different species belonging to the genera in question—*Monas crepusculum*, Ehrbg., *M. globulus*, Duj., *M. lens*, Duj., *M. elongata*, Duj., *Bodo socialis*, Ehrbg., *B. intestinalis*, Ehrbg., *Cercomonas biflagellata*, Stbg., *C. acuminata*, Duj., *C. globulus*, Duj. As I have had no opportunity of studying this memoir, which is but little known in Germany, I can offer no opinion as to the extent to which these forms really differ, nor as to the accuracy with which they are defined. But I think it necessary to point out that the species mentioned by Steinberg have hitherto, with few exceptions, only been observed living freely (*Monas globulus* even in sea-water). Although this fact as to the known mode of life of Monads by no means excludes a more or less frequent parasitic occurrence, it appears to me in the meantime questionable, especially considering the extreme difficulty of investigation and determination, whether we are justified from these data alone in reckoning the forms mentioned as human parasites. Yet Steinberg's researches are sufficient to prove that the cavity of the human mouth, with the putrefying organic remains and deposits between the teeth (in caries also in the interior), may be a fertile breeding-place for Monads. The same holds true, as we shall afterwards see, in regard to the genus *Trichomonas*.

Not less doubtful than the above forms are those Monads identified by Wedl as *Bodo saltans*, Ehrbg. (0·006 mm., Fig. 118), and *Monas crepusculum*, Ehrbg. (0·004 mm.), which are described by him as occurring often in great numbers upon unhealthy ulcers.[2]

Another Monad—*Bodo urinarius*[3]—which, according to the statements of Hassall, occurs very often in cholera patients, but only in albuminous alkaline urine, or along with *Vibriones*, can as yet hardly be accurately determined. It is described as an oval or round granular body of 0·0012 mm. in length and 0·0007 mm. in breadth, which moves quickly by means of two (sometimes three, or only one) flagella, and multiplies by division. Monads should only rarely be found in normal human urine, since it is only the intermingled organic sub-

[1] *Walter's Journal of Modern Medicine*, Nos. 20-24, 1862 (Russian), Kief.
[2] "Grundzüge der pathol. Histologie," p. 796.
[3] "General Board of Health," London, p. 293, 1855, and *Lancet*, Nov. 1859. *Schmidt's Jahrbücher*, Bd. cix., p. 157, 1861.

stances which make the existence of these parasites possible. But as such admixtures are more frequently found in the urine of animals (as Leeuwenhoek has shown in the case of the horse), the presence of these creatures is by no means rare in fresh urine.

Of all the parasitic forms described as occurring in man, there is only one which we know with tolerable accuracy—*Cercomonas intestinalis.* It is by no means identical, however, with *Trichomonas* (Fig. 119) and *Hexamita* (Fig. 120), mentioned by Ehrenberg and Dujardin as belonging to the same species, and already referred to as living in the cloaca of frogs and newts. Further, all the human parasites found in diarrhœtic stools, and described as *Cercomonas intestinalis,* do not, as we shall afterwards see, really belong to this species.

Cercomonas intestinalis, Lambl.

Davaine, *Comptes rendus Soc. biolog.*, 1854, "Traité des Entozoaires Synops.," ed. 2, p. xxiii., 1854 (*Cercomonas hominis*).

Ekeckrantz, "Bidrag till kännedomen om de i menniskans tarmkanal förekommande Infusorier," *Nordisk med. Arkiv*, Bd. i., No. 20 (*Virchow-Hirsch, Jahresber.*, Bd. i., p. 202, 1869).

Tham, "Tvänna fall af Cercomonas," *Upsala läkare Fören. Förhandl.*, Bd. v., p. 691 (*Virchow-Hirsch, Jahresber.*, Bd. i., p. 314, 1870).

Lambl, "Cercomonas et Echinococcus in hepate hominis," *Russian Medical Report*, No. 33, 1875 (Russian).

Zunker, "Ueber das Vorkommen der Cercomonas intestinalis im Digestionskanal des Menschen und deren Beziehung zu Diarrhöen," *Deutsche Zeitschr. für praktische Medicin*, No. 1, 1878 (*pro parte*).

[Grassi, "Intorno ad alcuni protisti endoparassitici," *Atti. Soc. Ital. sci. nat.*, vol. xxiv., pp. 12-22, 1882.—R. L.]

The body is generally pear-shaped, and bears a rigid terminal filament almost as long as itself, in addition to the much longer and very delicate vibrating whip-shaped flagellum.

As I have already said, *Cercomonas intestinalis* is known "with tolerable accuracy," and this is due to the descriptions of Davaine, whose observations, although the oldest on the subject, are still the

FIG. 121.—*Cercomonas intestinalis.* *A*, larger, and *B*, smaller variety. (After Davaine.)

most exact and best we possess (Fig. 121). Yet even Davaine distinguishes two varieties of these forms, differing from each other in form

and size, and perhaps even in the structure of the flagellate apparatus, so that one of them (the smaller variety) is almost nearer to the genus *Amphimonas*, Duj. = *Bodo*, Ehrbg.

The larger variety, whose length varies from 0·01 to 0·012 mm., was very frequently found in the stools of patients during the cholera epidemic, and often in such numbers that a single drop would contain several of them. The body was pear-shaped, and had in front a longish structure ("trait longitudinal"), which appeared almost like a mouth. A nucleus could hardly be distinctly seen. The little animals generally moved with great speed, but often attached themselves firmly to foreign bodies by means of their terminal filaments, and then exhibited a pendulous swinging instead of a progressive motion.

The second small variety, which was only once observed in a case of typhus—but on this occasion in great numbers—had a rounder body (0·008 mm.) and two flagella of indefinite length, one in front and one behind, but both situated somewhat to the side. The motion is described as extremely rapid.

It is still, however, a moot-point whether these two varieties are really different. The illustrations which we have reproduced show only slight variations; and the difference in the structure of their appendages, which alone could be of any significance, is so slightly established by Davaine, that for the present no importance can be attached to it. Hence, later observers have classed these two varieties together again without further discussion. They also recognise only a single *Cercomonas intestinalis*, namely, "that observed by Davaine." [Grassi (*loc. cit.*), too, observed variations in form and size in his *Cercomonas* (*Monadacomonas*), but nevertheless speaks of another, which he refers to our *Trichomonas intestinalis*.—R. L.] It is true that a second form, which we shall soon consider, has been noted by other investigators, and especially by Zunker; but they have made no attempt to identify it with the different varieties of Davaine, but have rather sought to establish its claims as a separate species.

These later observations have also shown that the occurrence of *Cercomonas intestinalis* is much more frequent and extensive than the communications of Davaine led one to suppose. Not only is the parasite found in the intestine (or in the excrement) in cases of cholera and typhus, but also in other diarrhœtic conditions,[1] whether these are dependent upon an acute or on a severe chronic disease. Lambl,

[1] Lösch holds (*loc. cit.*) the occurrence of Monads to be quite common in dysenteric stools. [Grassi observed *Cercomonas* in different parts of Italy more than one hundred times in the course of a few months. Cunningham also alleges that this parasite is exceedingly common in India (especially in alkaline fæces), and is not unfrequently found in quite healthy individuals.—R. L.]

who observed these parasites in myriads in the jelly-like intestinal mucus of children as early as 1859, but published then only a very insufficient description of them,[1] mentions afterwards, in the paper cited, a case in which *Cercomonas intestinalis* (or at least a form which cannot by our present means be distinguished from *C. hominis*) was found even in the liver.

The person infested was a patient suffering from *Echinococcus*, who died in consequence of the treatment (with caustic paste). On a *post mortem* examination twelve hours after death a large *Echinococcus* (32 cm. long, 18 to 20 cm. broad) was disclosed in a cyst, apparently formed from a widened and degenerated bile-duct, and containing a

FIG. 122.—*Cercomonas* from the liver. (After Lambl.)

slimy liquid, in which were, besides *Vibriones* of diverse sizes, a countless number of living specimens of *Cercomonas*. This fluid, together with the contents of the bladder-worm, yielded sediment of nearly 500 c.c., in which the animals occurred in such abundance that a large number were to be found in every drop. They generally showed an extremely quick, but very variable motion, and sometimes hung grouped together in dozens around a common centre.

The size varied exceedingly between the limits of 0·005 and 0·014 mm. The form also varied according to the contraction of the body, but was generally elliptical or spindle-shaped, or sometimes rather pear-shaped or cylindrical. Flagellum and terminal filament could be distinctly demonstrated, although the former was extremely fine, and although instances occurred in which both appeared to be wanting. Lambl, who, it may be remarked, cites his colleagues at Warsaw as wit-

[1] *Prager Vierteljahrsschr. f. prakt. Heilk.*, Bd. lxi., p. 51, 1859; Aus dem Franz-Joseph-Kinderspitale in Prag., Bd. i., p. 360.

nesses of his observation, thought he could distinguish a ventral and dorsal surface in the parasites which he kept alive for a week in their usual liquid. The latter surface has, he says, a firmer parenchyma and smoother contour, while the ventral is softer and more mobile. This appearance of greater mobility arises partly from the play of an opening situated at the base of the flagellum, which obviously represents a mouth, and is surrounded by contractile borders. Besides some strongly refractive granules, two pulsating vacuoles could be distinguished in the hyaline parenchyma posteriorly.[1] A division was also observed, both in the mobile forms and in those which had contracted into a ball, and had lost apparently both flagellum and tail. Finally, the twin forms are connected together only by a thin thread, which has been regarded as the flagellum.

Even if the reproduction of *Cercomonas* had not been directly observed, yet the consideration of its occurrence in immeasurable numbers would have necessarily led us to the same result. The possibility of an oft-repeated and sustained importation, which one could perhaps admit when the parasites inhabit the intestine, is here excluded by the facts of the case. Not only because the patient, a gardener, spent the last two months of his life in the hospital, in which such an importation could hardly take place, but, still more cogently, because on *post mortem* examination the parasites were found exclusively confined to the *Echinococcus*-sac, not a trace of them being found in the intestine. We must of course suppose that the *Cercomonas* had penetrated into the liver from the intestine, but that had probably taken place a long time before, perhaps at the commencement of the *Echinococcus*-disease, which had lasted for five years, according to the patient's report. Perhaps at that time the patient harboured the *Cercomonas* throughout the whole intestine, and the hepatic parasites, becoming continually more perfectly encapsuled by the *Echinococcus*-cyst, are to be regarded as the last survivors of a previous intestinal disease.

Be this as it may, this much is certain, that the case here cited is not merely the only one of the kind, but has also a special interest in connection with the history of *Cercomonas*.

The cases observed by Ekeckrantz, Tham, and Zunker of *Cercomonas* in the intestine occurred in individuals who had all suffered

[1] According to Zunker's description, *Cercomonas intestinalis* has "a longish, oval body, pointed behind, of 0·01 to 0·013 mm. in length; at the posterior end is a strong spine, and at the anterior a long flagellum, not measurable on account of its constant motion. It has also granules lying in a transparent body, and generally a single vesicular nucleus." A second form, only twice seen by Zunker, along with other intestinal Monads, is compared to the *Monas lens*, Ehrbg. It had only a third the dimensions of the common *Cercomonas*, and a round body, which showed no differentiation, and was in constant motion.

for years from dyspepsia and diarrhœa. The stools were usually peculiar, of a brownish-yellow colour and heavy putrid smell, and generally, in spite of their thin, pulpy consistence, of a toughish character, which probably arose from the presence of numerous masses of mucus. Under these circumstances, the examination of the fæcal masses is sufficient to establish the diagnosis of *Cercomonas* with tolerable probability, especially since this parasite seems never to occur in the ordinary forms of diarrhœa or in normal stools.

That the presence of the parasites has a certain connection with intestinal disease cannot be denied, since, according to the unanimous testimony of the investigators, the intensity of the latter is proportional to the frequency of the *Cercomonas*, since an increase in the number of the parasites was always accompanied by an aggravation of the disease, and recovery only took place on their disappearance.

In spite of this, however, it would be unsafe to refer the intestinal unhealthiness exclusively to parasites. At any rate, a link is still wanting in the chain of proof. Until this is supplied, it seems more probable to suppose that the mucous masses produced by diarrhœtic conditions supply a favourable breeding-place for the parasites (as was similarly noted in the case of the so-called *Bodo urinarius*), and that they sometimes promote their increase to such an extent that they become a decided irritant, and thus tend to aggravate the disease.[1]

In one case of a patient suffering from Carcinoma ventriculi, Zunker observed this parasite even in the mouth, among the fur covering the tongue, but in the thin pulpy stools only a few specimens could be found.

Trichomonas, Donné.

The oval body is provided not only with a flagellum, usually double or triple, but also with a longitudinal fringe or undulating comb.

The genus, which we have shortly characterised above, was founded on a parasitic Monad, living in the human vaginal mucus. For a time it appeared as if this form (*T. vaginalis*) was to remain the only one of its kind, until Dujardin discovered a second (*T. limacis*) in the intestine of the field-slug. Other species were afterwards added to the genus, but all which have been found and described are parasites, and indeed intestinal parasites, so that there are apparently no free-living *Trichomonades*. We now know that they occur

[1] [Grassi and Cunningham are both disposed to deny any pathogenic significance to the *Cercomonas*.—R. L.]

both in Invertebrata (for example in the rectum of the larva of the cockchafer) and in Vertebrata, both in cold-blooded (*Trichomonas batrachorum*) and in warm-blooded animals, and especially in mammals, as in the stomach of the pig and the intestine of the guinea-pig. Nor is it to be denied that some of the forms in the human intestine described as *Cercomonas* belong to this genus.

After the observations which Stein has published concerning *Trichomonas batrachorum*,[1] some modification must be made in the opinion hitherto held by all investigators in regard to the structure of the lateral comb, so characteristic of this order. For this does not consist of single short filaments in a row near each other, but of an undulating membrane, the vibrations of which easily gave rise to the idea of ciliary motion. Here I may mention the familiar spermatozoa of the salamander, whose fringed edges were also long referred to the possession of cilia. According to Stein, however, the definition of it as an undulating membrane is not perfectly correct. It should rather be said that the extremely soft body rapidly pushes out, one after another, tooth-like or rounded processes, which together produce the impression of a wave ceaselessly running from front to back, along the margin of the body, or "as if this were provided with a toothed undulating membrane." It is not easy to see how this conception can agree with the fact that the apparatus in question also appears

FIG. 123.—*Trichomonas batrachorum* (after Stein).

in dead animals in the form of an irregularly waving margin, which, as I further note, allows itself to be stained *in toto*. [This has recently been stated by Blochmann[2] in opposition to Grassi (*loc. cit.*),

[1] *Loc. cit.*, p. 79. [2] *Zeitschr. f. wiss. Zool.*, Bd. xl., p. 42, 1884.

who regards the ciliary comb as a long flagellum directed backwards, and refuses to recognise the genus *Trichomonas*.—R. L.] On this ground also, I believe that *T. batrachorum* not merely seems to have, but really has, a vibrating membrane. I am further confirmed in this opinion from the fact of an Infusorian with a ciliated border having been formerly found by Eberth in the Lieberkühnian glands of the alimentary canal of hens and ducks (Fig. 124), which probably, too, was nothing but a *Trichomonas*, in which the presence of the flagellum was overlooked.[1]

FIG. 124.—Infusorians with undulating longitudinal membrane from the intestine of the hen (after Eberth).

Since *Trichomonas batrachorum* is, on account of its considerable size, a much more convenient object than the human *Trichomonas*, we may assume for the latter the same structure of the accessory ciliated apparatus, although we must leave it to the future to justify this procedure.[2]

Trichomonas vaginalis, Donné.

Donné, "Réch. microscop. sur la nature du mucus :" Paris, 1837.

Idem, "Cours de microscopie," pp. 157-161, Fig. 33, 1847.

Kölliker und Scanzoni in Scanzoni's "Beiträgen zur Geburtskunde," t. ii., pp. 131-137, tab. iii., Fig. 2 : Würzburg, 1855.

Hausmann, "Die Parasiten der weiblichen Geschlechtsorgane," p. 42 : Berlin, 1870.

Hennig, "Der Katarrh der innern weiblichen Sexualorgane," p. 66 : Leipzig, 1870.

[Blochmann, "Bemerkungen über einige Flagellaten," *Zeitschr. f. Wiss. Zool.*, Bd. xl., p. 42, 1884 (with Fig.)].

This form has a somewhat bulging, oval body, on an average about 0·015 *mm. long, not including the terminal filament, which is half the length of the body. The flagella, which do not exceed the whole body in length, are generally three in number. The lateral undulating comb reaches from the anterior margin to about the middle of the body, and*

[1] Stein, who expresses the same opinion, blames me for having "immediately" made a separate genus (*Saenolophus*) of this parasite (see the first German edition of this work, p. 140). In exculpation, I may state that at that time, when the structure of the accessory ciliated apparatus of *Trichomonas* was still unknown, the Infusorian described by Eberth stood completely isolated, and therefore had to be regarded as the representative of a special genus.

[2] [This has been confirmed by Blochmann (*loc. cit.*).—R. L.]

is said by older observers to consist of six or seven short hairs, which are in constant vibration. The parenchyma is colourless and clear, with fine granules in the interior (*Fig.* 125).

As will be seen from the foregoing diagnosis, our knowledge of the vaginal Monads has only reached a satisfactory state in consequence of Blochmann's researches. Even the number of the flagella was uncertain, being supposed to vary from one to three. Where apparently only one is present, they have probably coalesced, as may be guessed from the fact that in such cases the flagella are sometimes represented as divided at the end. A fine longitudinal line running down near the accessory cilia is interpreted as the mouth, with what accuracy is a moot-point; it might more probably represent the point of attachment of the ciliary comb. [In the anterior end is a distinct nucleus (Blochmann)].


FIG. 125.—*Trichomonas vaginalis.* (After Kölliker.)

Some investigators assert that they have seen forms of *Trichomonas* which were in a state of greater or less expansion, and were furnished with stiff, bristly hairs, and have even tried to make a particular species of them. To all appearance, however, these statements deserve but little confidence. These parasites are extremely sensitive to water and watery solutions, and generally perish quickly after the application of such fluids. They then swell up, and coagulate into a more or less globular mass—motionless, and robbed of its appendages. As these much altered forms have a certain resemblance to ciliated cells, it is very likely that they were the origin of the above statements, just as in earlier times they gave rise to the very widely spread opinion, held by many weighty authorities (such as Valentin, Siebold, and others), that the *Trichomonas* of Donné represented only isolated and altered ciliated cells.

In their natural condition the vaginal Monads show a quick and lively motion, which, when the parasites are present in great numbers, almost gives the impression of the so-called Infusorian "swarming," and especially since the animals frequently crowd round a lump of mucus, or are united into a group by means of their tails. The motion also changes, more or less, as the body turns first right, then left, in consequence of the influence exerted on it by the undulations of the ciliary comb. [These forms have also a creeping motion like *Euglena.*] If the surrounding temperature be reduced, the motion becomes slower, and entirely ceases a few minutes after 9° C. is reached, but recommences as soon as heat is again applied.

Nothing is known regarding the reproductive process, for though Hennig mentions having seen two animals hanging firmly together by their tails, and interprets the process as an act of copulation, it might very probably merely represent the result of division.

Donné, who first discovered these parasites in women suffering from gonorrhœa, thought for some time that he could attribute a diagnostic value to them, but afterwards convinced himself that they occurred quite as frequently in uninfected persons. In quite normal vaginal mucus, containing only separated epithelial cells, but no mucus nor pus corpuscles, the parasites indeed appear to be absent. But in increased secretion, especially of the mouth of the womb and upper part of the vagina, they become quite frequent, and are the more likely to occur when the secretion gives a strongly acid reaction, is of a creamy nature, and rich in pus corpuscles. Kölliker and Scanzoni found these parasites in the majority of persons whom they examined, and during pregnancy as well as at other times. Hausmann mentions that he found them thirty-seven times in two hundred pregnant women, and forty times in one hundred not pregnant. In the secretion of the cervix, which differs both chemically and histologically from the vaginal mucus, *Trichomonas* is never found.

Trichomonas intestinalis, Leuckart.

Marchand, *Archiv f. pathol. Anat.*, Bd. lxiv., p. 294 (*Cercomonas intestinalis*), 1875.
Zunker, *Zeitschr. f. pract. Medicin*, No. 1, p. 1, 1878 (*pro parte*).

This species resembles the above in size, form, and in the possession of a tail, but is destitute of flagella (?). The ciliary comb is distinctly developed, and seems to consist, as the accompanying illustration shows, of at least twelve hairs (*Fig.* 126.)

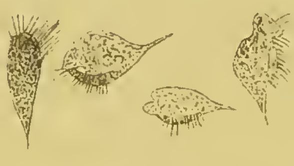


Fig. 126.—*Trichomonas intestinalis* (after Zunker).

I think I am not mistaken in referring to the genus *Trichomonas* yet another Infusorian form,[1] which was first found by Marchand in the stools of a typhus patient, and afterwards by Zunker in severe intestinal disease, but was looked upon by both as a *Cercomonas*. It is true that neither of the two observers mentions the flagellum, which must be regarded as a characteristic mark of *Trichomonas*; but it is probable that they

[1] Stein wished also (p. 40) to claim the *Cercomonas intestinalis*, first found by Lambl in the small intestine of a child, as a *Trichomonas*, but Lambl himself fterwards established its identity with the *Cercomonas* from the *Echinococcus*-tumour, so that it is a genuine *Cercomonas*.

merely overlooked the two closely approximated thin threads, as has often been done in similar cases even by skilful investigators. Apart from this, the parasite in question has so striking a resemblance to *Trichomonas vaginalis*, that the two forms could hardly be distinguished, if the accompanying plates did not show the ciliated fringe of *Trichomonas intestinalis* consisting of a much larger number of cilia.

The form of the mobile animal in its condition of rest is, according to Zunker, best compared to a somewhat long almond kernel. It consists of a transparent mass of protoplasm, which contains, besides some irregularly scattered granules, one or two vesicular structures (vacuoles ?) lying in the pointed posterior end of the body. At the posterior end there is also a short spine-like process, while the rounded-off anterior portion seems to exhibit a very distinct row of cilia, which by their rapid action produce a continuous undulating motion. Under favourable circumstances the animals were extremely lively. They moved with great rapidity, and also possessed great contractility, so that the form of the body often changed in an almost amœboid manner. The dimensions varied from 0·007 to 0·01 mm. in breadth, and from 0·01 to 0·015 mm. in length, exclusive of the long tails, which were from 0·002 to 0·003 mm. long. The nearer the time of death approached, the weaker the motions became. The animals remained upon the same spot, turned round in a circle on the anterior end, or swung like a pendulum, using the caudal extremity as a point of support. Finally, they sank down motionless, lost the ciliary comb, and assumed a round shape, most deceptively like the dull granular clotting of a cell. The rapidity with which death followed depended very essentially on the surrounding temperature, just as we noted before in the cases of *Trichomonas vaginalis* and *Cercomonas intestinalis.*

What has been previously observed as to pathological and clinical significance, and as to the nature of the Monad-containing fæces in the case of *Cercomonas intestinalis* (which, according to Zunker, seems much more rare than *Trichomonas,* since he only observed it twice and *Trichomonas* seven times), is so perfectly applicable to this second species that I shall content myself with referring to it. But this much may be added, that this *Trichomonas* occurred in acute cases of typhus, peritonitis, and in severe diarrhœa, complicated by icterus and pneumonia, as well as in chronic ailments (which were again generally diarrhœtic).

In conclusion, I may note that *Trichomonas intestinalis,* like *Cercomonas intestinalis,* is probably sometimes found in the human mouth. I base this supposition on the researches of Steinberg, who, in the above-mentioned treatise on the microscopic character of the dental

deposit in men, mentions no fewer than three species of *Trichomonas*, which are respectively described under the names of *T. elongata*, *T. caudata*, and *T. flagellata*.

Order II.—Ciliata.

Stein, "Der Organismus der Infusionsthiere:" Abth. i., 1859; Abth. ii., Leipzig, 1867.

Infusoria with numerous cilia, which are never confined to the immediate neighbourhood of the mouth, but either cover the whole body or are disposed in greater numbers, and in more regular groups on the anterior portion, or on the ventral surface. The body-parenchyma exhibits, as a rule, a distinct differentiation into a cortical layer and central mass, and usually contains a nucleus and accessory nucleus. When a mouth is present there is also an anus.

This division contains the larger and more highly developed Infusorians, the properly typical forms with respect to which what we have before remarked in regard to reproduction and multiplication primarily and specially holds good.

Although agreeing in certain essential conditions, the Ciliata show manifold differences in the details of structure, not only in the above-mentioned ciliary apparatus, but in form and habit, and especially in the mode of motion. Some have attempted to turn these differences to account by dividing the Ciliata[1] again into a number of sub-orders. Thus they distinguish in the first place a group "Holotricha," so called because the generally flattened and oval body is covered throughout its whole extent by a thick coating of short cilia. In the group "Heterotricha" there is, in addition to this covering of cilia, a peculiar modification of the oral region, which develops by flattening or by excavation into a larger and smaller peristome. This peristome is sometimes indicated even in the Holotricha, but in the Heterotricha it is always distinguished by one of its edges being furnished with a longer or shorter, and sometimes spiral, row of strong cilia, which can be traced as far as the mouth aperture. In the so-called "Peritricha" this peristomial region surrounds the whole anterior end of the body, which thus possesses a complete girdle of cilia, and can also be retracted to a greater or less extent into the other portion of the body. In individual members of this group an aboral girdle of cilia occurs, in addition to the cilia of the peristomial region, while the former uniform ciliated coat is completely absent. The body has besides a cylindrical form, so that the structure appears somewhat

[1] The altogether unciliated adult Suctoria, or Acinetans, are not taken into account, as they never appear as parasites in the Vertebrata.

radiate. Unlike the members of the last group, the so-called "Hypotricha" are bilaterally symmetrical with flattened body and an arched back. The latter is completely naked, for the cilia, which are partly in the shape of stylets and hooks, are developed exclusively on the ventral surface, on which the mouth is also found. With the help of these appendages, the animals exhibit a regular creeping motion.

All these groups, with the exception of the last, contain, besides free-living forms, parasitic species, which infest both the higher and lower animals. Thus the paunch and reticulum of the sheep and ox harbour no fewer than six different species of ciliated Infusorians, and that in such abundance and constancy, that they are always to be found, along with the above-mentioned Monads, in countless numbers in every individual. Five of these (species of *Ophryoscolex* and *Entodinium*) are remarkable mail-clad forms with retractile organs, and belong to the Peritricha; the sixth (*Isotricha intestinalis*) is one of the Holotricha.[1] Along with the latter we must include the mouthless genus *Opalina*, which has, however, been hitherto observed only in cold-blooded animals, but is very often found as constantly and frequently[2] in the cloaca of the Batrachia, and especially of the common frog, as are the formerly mentioned parasites in the ruminants. Along with the *Opalinæ*, other heterotrichous parasites are found in the frog, all which forms were referred by Ehrenberg to the great genus *Bursaria*, but we now know that they belong to certain exclusively parasitic groups (*Balantidium*, *Nyctitherus*) which are nearly related to *Bursaria*, and which form along with them the family of the Bursarieæ.

To this family, and indeed to the genus *Balantidium*, we must also refer the so-called *Paramœcium coli*, the only ciliated Infusorian which has been as yet found in the human body. Other ciliated forms have, it is true, been observed in men, in unclean wounds, ulcers, &c., but always only free-living forms, which generally live on putrefying matter, so that, in spite of their occurrence in this way, they ought hardly to be reckoned among genuine parasites. J. Vogel mentions among these forms *Colpoda cucullus* and *Vorticella*,[3] which are both extremely common in putrid infusions. Wedl also mentions a *Bursaria* (?),[4] but from the "flapping" motions of the lips of the

[1] Regarding these species see the statements of Stein (*Lotos*, Jahrg. ix., pp. 55, 1859, and *Abhandl. der kgl. Böhmischen Gesellsch.*, Bd. x., p. 69, 1860). In the colon of the horse there very often occurs a hitherto but little known Infusorian, which, so far as regards the nature of its cilia, might belong to the above-mentioned genus, *Isotricha*, or *Balantidium*, and at any rate possesses a completely ciliated oval body.

[2] The parasitic Infusoria of the frog were detected even by Leeuwenhoek, "Op. omn., Anat. et Contempl.," t. i. p. 56, 1722.

[3] "Pathologische Anatomie," Th. i., p. 404, 1845.

[4] "Grundzüge der pathol. Histologie," p. 796, Fig. 195.

slit-like mouth, I am inclined to think that this species is simply the very common *Glaucoma scintillans*, Ehrbg.

Family BURSARIEÆ.

Heterotrichous Infusoria, with a sometimes oblique, sometimes straight, peristomial cleft, which runs from the anterior end of the egg-shaped body, generally on the right side of the ventral surface, as far as the mouth, and is bordered only on the left side by the adoral cilia.

Balantidium, Claparède and Lachmann.

The body is egg-shaped, or rather longer, with ventral and dorsal surface almost equally arched, anteriorly somewhat truncated, and provided with a peristomial region, which narrows posteriorly, and only deviates slightly towards the right side of the ventral middle line. This asymmetrical condition is most striking in a state of rest, when the peristome is bent together into a trough-like shape. The adoral cilia of the left peristomial border differ only slightly in length and strength from the cilia of the body. The mouth occupies the deepest part of the peristomial region, and is continued into the interior by a short gullet. The anus at the posterior end of the body is recognisable by the escape of excrement. There are generally two or three contractile vesicles. The nucleus is of an oval or short ribbon-like form. All the species live parasitically in the alimentary canal of the Vertebrata, especially in the naked Amphibia.

The genus *Balantidium* was instituted by Claparède and Lachmann,[1] for the reception of Ehrenberg's *Bursaria entozoon*, but was erroneously credited with styliform cilia on both borders of the peristomial notch. Stein was the first to recognise the true nature of the peristome, and he increased the number of species, partly by new discoveries, and partly by proving that the so-called *Paramæcium coli* also belonged to this genus.

Balantidium coli (Malmsten), Stein.

Malmsten," *Archiv. f. pathol. Anat.*, p. 302, Bd. xii., 1857 (*Paramæcium coli*).

Leuckart, "Parasiten," first German edition, Bd. i., p. 146.

Stein, "Organismus der Infusorien," Abth. ii., p. 320.

Ekeckrantz, Bidrag till kännedomen om de i menniskans tarmkanal förekommande Infusorier," *Nord. med. Arkiv*, No. 20, Bd. i., 1869.

Wising, "Till kännedomen om Balantidium coli hos människan," *ibid.*, Bd. iii., No. 3, 1871.

Infusoria with a short oval body (of 0·07 *to* 0·1 *mm. long by* 0·05 *to* 0 07 *mm. broad); the anterior end somewhat truncated, with a very short*

[1] Études, *loc. cit.*, t. i., p. 247.

peristome, which usually extends to the right of the middle line, in the form of a funnel, narrowing to a small cleft, and leading into a short gullet. While feeding the peristome is broadened out, so as to look like a triangular surface, sloping away obliquely towards the anterior border.

FIG. 127.—*Balantidium coli*, with widely opened peristome (dorsal view).

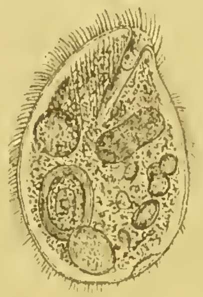


FIG. 128.—*Paramæcium* (?) *coli.* (After Malmsten).

The nucleus is elliptical, and slightly bent, two sluggish contractile vacuoles usually lie on the right side, one behind, the other further forward. The anus is hardly perceptible.

Balantidium coli (Fig. 127) was first detected in 1856 by Professor Malmsten, in Stockholm, in the stools of a man who had two years before suffered from a violent attack of cholera, and had since continually complained of dyspepsia, and was alternately affected with constipation and with painful diarrhœa. On examination of the rectum there was seen, about an inch above the anus, a small sore, which produced a purulent secretion, mixed with blood; in this the Infusoria were found in large numbers. Even after the wound healed the former troubles remained, and the Infusoria were still found in the fæces and intestinal mucus. Even at the time of discharge the almost convalescent patient was still infested with the parasites, although their number had considerably decreased. The investigation of the Infusorian was undertaken with the help of the famous zoologist Lovén, and it was he who recognised it as new, and referred it (Fig. 128) with some hesitation to Ehrenberg's holotrichous genus *Paramæcium.* Soon afterwards the parasites were abundantly observed in a woman who had suffered for years from a severe intestinal trouble, and who applied for treatment enfeebled by continual diarrhœa, with bloody and purulent stools. The patient died after a short time. During the last stages of the disease the fæces had been voided involuntarily, and with a fearful stench. *Post mortem* examination showed numerous small gangrenous ulcers in the large intestine,

which was, from the sigmoid flexure onwards, filled with stinking pus. At these places but few Infusoria were found, but they were present in immense numbers over the whole of the sound mucous membrane of large intestine, as also in the cæcum and vermiform appendix. There were none to be found either in the small intestine or in the stomach.

Stein has made it probable that this parasite had perhaps been previously observed, and that by the great discoverer of the Infusoria —Leeuwenhoek himself. The latter at least reports[1] that, once having had for a lengthened period abnormal stools, he made an examination of them, and observed delicate mobile organisms, mostly about the size of a blood corpuscle, but some larger, which moved about with the aid of a little foot-like hook. In small portions of the fæces, as large as a grain of sand, there was at least one of these little animals, but generally more—four or five, or even eight. These never occurred in the normal excrement. Since the *Balantidia* are considerably larger than a blood corpuscle, Leeuwenhoek's description seems but slightly applicable; but probably the report as to the size was based on a merely subsequent estimate, in which a mistake might easily be made; and it is indeed impossible that Leeuwenhoek, with the optical appliances at his disposal, could have seen the movement of cilia, which he describes, in an Infusorian, as only the size of a blood corpuscle.

The observations of Malmsten still stood alone when I stated, in the first edition of this work (1863), that man was not the only host of the so-called *Paramæcium coli*, but, on the contrary, that it also occurred in swine, and was in fact found constantly, and in extraordinary abundance, in the colon and cæcum of these animals. In order to see the parasites, one has only to take a probe and remove some dung or mucus from the rectum. Even with a lens one can distinguish colourless Infusoria moving here and there about the dung.

Since my results have been corroborated in various parts of Germany, in Sweden (by Stein, Ekeckrantz, and Wising), and in Italy (Grassi), we may conclude that the pig is the proper host of *Balantidium coli*, and that man only occasionally derives it from the latter, and under favourable circumstances harbours it for a while. In harmony with this is the fact that the *Balantidium* in man has an average size of 0·06 to 0·07 mm. (according to Wising), which is a little less than that of the forms found in the pig.

In the meantime, however, the cases investigated by Malmsten have not remained solitary. Stieda[2] first observed the occurrence of

[1] *Loc. cit.*, Part ii., p. 37.

[2] *Archiv f. pathol. Anat.*, Bd. xxxv., p. 139, 1865.

Balantidium in two cases of typhus in the Dorpat Hospital, and Ekeckrantz,[1] Belfrage,[2] Windbladh,[3] and Wising[4] soon reported four more instances. The number of cases was afterwards doubled by Petersson[5] and Henschen,[6] so that apparently *Balantidium* does not belong to the rarer human parasites. The *Balantidia* were always found in individuals affected with more or less obstinate diarrhœa, and once in association with numerous ulcers, especially of the cæcum, which finally led to the death of the patient (Belfrage's case). In one case Henschen observed a complication with acute stomachic and intestinal catarrh, but this was perhaps an exception.

It is a striking fact that all the cases of *Balantidium coli* as yet observed have been confined to a somewhat restricted geographical area. No case of this kind has yet been observed in Germany, England, or France,[7] although the examination of the fæces has been prosecuted at the universities in these countries as well as in Stockholm, Upsala, and Dorpat, and although the swine are probably, and in Germany certainly, infested with these parasites. The reason of this limited distribution in space can only be sought in local conditions. There must be certain habits of life which determine the occurrence of the parasite, but without more intimate knowledge of the circumstances we can hardly enter into details. Only this much is clear, that the explanation is to be sought primarily in the relations between men (especially in their food and drink) and the swine, which, in the localities referred to, are probably fattened in the houses.

Structure and Mode of Life.

The ease with which we can procure specimens of *Balantidium coli* from pigs has of course aided the progress of our knowledge of its structure and life-history, so that this is at present, though not indeed perfectly complete, at least satisfactory.

The Body exhibits great permanency of form—greater at least than we are wont to find in the naked Infusoria. This is specially true of those specimens which are distended with food, and easily detected by their compressed oval form and rounded posterior ex-

[1] *Loc cit.*

[2] "Fall af Balantidium coli," *Upsala läkareffören. Förhandl.*, Bd. v., p. 180.

[3] "Fall af Balantidium coli," *ibid.*, Bd. v., p. 619.

[4] *Loc. cit.*

[5] *Upsala läkareffören Förhandl.*, Bd. viii., p. 251, 1873 (three cases).

[6] "Fran Dr. Waldenströms Poliklinik," *ibid.*, Bd. iv., 591 (one case); and "Fem nya Fall af Balantidium coli," *ibid.*, Bd. x., p. 123 (five cases).

[7] [Grassi states (*loc. cit.*, p. 67) that Dr. Graziadi found *Balantidium* in one of the chlorotic patients at the St. Gotthard Tunnel; and Treitte also reports it from Cochin-China (*Archiv. méd.*, t. xi., pp. 129-133, 1877).—R. L.]

tremity. But even the more slender specimens exhibit on the whole but slight contractility, and are never specially lively. The most striking movement one sees is that of the peristome and anterior end of the body, which sometimes stretches out like a neck, and bends round towards the somewhat less convex ventral surface.

This is correlated with the nature of the body, which has its inner parenchymatous substance packed full of food, leaving only the front part of the body unoccupied, and reducing the cortical layer to a comparatively thin sheath. It is, however, well defined, since the two masses differ widely in nature and appearance, and are sharply distinguished from one another.

The Interior Mass consists of a substance finely granular throughout, in which one can distinguish fat granules of varying size, and, especially in the posterior half, one or two larger granular bodies (fæcal masses?). Occasionally, too, one sees a starch granule, especially when the pigs are feeding copiously on potatoes. Wising has also observed red and white blood corpuscles (pus corpuscles?) in the interior of the *Balantidia* infesting the human intestine. Since, on the whole, but few firm and definite bodies are found in these animals, we may perhaps conclude that their food consists mostly (as in the other species of *Balantidium*) of the more pulpy contents of the intestine. In contrast to the thick interior substance, the cortical layer consists of a clear, almost transparent, protoplasm, exhibiting that striated appearance which often occurs, and more conspicuously than in the present case, among the Infusoria. The striæ all start from the peristomial region, and run in long spiral lines to the posterior extremity. They are most distinct in front, and in their arrangement present an almost radiate appearance. They consist probably of fine fibres, which are embedded in the cortical layer at equal distances from one another, and which squeeze the looser parenchyma between them into frills. At the anterior end of the body one can often see these frills in profile as little marginal knobs. On its surface the cortical layer bears a somewhat firm cuticle with cilia, which are, as Malmsten pointed out, more thickly arranged between the above-mentioned frills.

Observers are not altogether consistent in their descriptions and representations of the peristome. Previously to Stein's researches it was usually regarded as the mouth opening, and is so still by some (Ekeckrantz). This idea is tenable so long as one examines it only in its short and rudimentary state, but not when one compares it with the more developed peristome of other species. This comparison leaves hardly any doubt as to the fact that this structure forms part of the outer body-wall, a part, moreover, easily distinguishable from

the rest of the surface of the body, but leading so gradually into the mouth that it seems to represent only a sort of pre-oral cavity.

The Peristome (Fig. 130), as seen in these constantly rotating animals, usually appears as a conical shell, with a slit running up its whole length, opening to the exterior at the right side of the anterior pole, and thence extending obliquely towards the median plane. The narrowed posterior end is continued further into a short gullet, which is never absent (as Stein alleges), but can be followed plainly to the anterior limit of the medullary substance, into which it distinctly sinks. The more or less widely gaping slit of the peristomial funnel, whose left border is beset by the adoral cilia, belongs to the ventral surface.

These conditions are entirely altered when one has the opportunity of observing the animal feeding. In this act the peristome (Fig. 127) broadens out by the unfolding of its lateral borders into a triangular space, which is recognisable as the anterior portion of the ventral surface obliquely truncated in a dorsal direction. The space is, moreover, almost symmetrical,[1] which shows that the left peristomial border exceeds the right in length and mobility, and therefore projects further out when the funnel is unfolded. The surface is by no means perfectly even, but sinks in posteriorly, so that it passes without any well defined boundary line into the above-mentioned gullet. One sometimes sees these animals creeping on their expanded peristome, as snails do on their foot, without in any way changing the position of the body. The adoral cilia keep up a lively motion, which sometimes looks like the rapid rotation of a wheel. The other cilia round the border are stronger and longer than those of the general body surface. On the other hand, the peristomial region itself is (according to Stein) destitute of cilia.

Besides the gullet (œsophagus) which runs obliquely through the cortical layer, we find internally a nucleus and contractile vacuoles, both of which, of course, belong to the ectosarc.

The Nucleus lies on the ventral surface, above the middle line, sometimes far forward, sometimes posteriorly. It is only faintly defined, pale, and homogeneous, extended, and not straight, but kidney-shaped. The median constriction, which Lovén and Wising thought they perceived, does not in reality exist. Nor have I been able to find a nucleolus, although Wising reports having several times observed it as a small round body beside the nucleus. Stein also has looked for it in vain.

[1] Deceived by such appearances, I have, in the first edition of this work, credited the so-called *Paramæcium coli* with a terminal mouth, and have suggested its association with the genus *Holophrya*, if, indeed, it were not preferable to erect it into a new genus.

The Vacuoles are usually two. One lies at the posterior extremity of the body, the other, separated from it by a varying distance, is further forward on the ventral surface. Sometimes a third is seen, and there are also cases in which only one is present—usually the posterior, which is generally the larger. Their state of tension varies exceedingly, and they become sometimes so full that the surrounding substance is protruded like a hump, or the whole body is deformed. The contractions are exceedingly slow and weak, so that they easily escape observation. One sometimes sees the

FIG. 129.—*Balantidium coli* in conjugation (after Wising).

vacuoles perceptibly changing their position, and wandering from one place to another. Stein observed them connected by a lacuna, and the contents of the anterior one being conveyed to the posterior. An opening to the exterior has not been observed.

The Reproduction of Balantidium coli exhibits, according to Wising, a process of conjugation (Fig. 129), in which the peristomial regions are closely fused with one another, while the bodies remain quite separate. The conjugating individuals present exactly the same appearance as Stein described in *Balantidium entozoon*, except that the changes of the nucleus and nucleolus, which occur normally in the latter, have not been observed by Wising. Indeed, only a few instances of conjugation have been observed, but quite enough to convert the *à priori* probable occurrence of the process into a certainty.

Division is much easier to observe than conjugation. It is transverse division which takes place here, as in the allied species, and indeed in the majority of the Infusoria. Stein, Ekeckrantz, and Wising have often observed it, and I have frequently noted it in my later investigations. As regards some points of detail, I am forced to differ somewhat from my predecessors. They describe the body of *Balantidium* as simply constricting itself in the middle, after previous growth in length, and then, along with the nucleus, separating into

two parts, of which the posterior subsequently forms for itself a peristome and an adoral zone of cilia. My observation was somewhat different, and agrees with Stein's account of the division of *Balantidium entozoon.* The first step in the division of the almost cylindrically extended body (0·15 mm.) is the formation of a ciliated circle, which surrounds the middle of the body, and comes short of the adoral cilia neither in size nor in lively motion. On the dorsal surface this girdle exhibits a considerable blank; it is therefore primarily and especially on the ventral surface that it originates, whether by new formation or by outgrowth of former hairs I must leave undetermined. The two vacuoles are widely separated, and the nucleus has grown comparatively little.

FIG. 130.—*Balantidium coli* in various stages of division.

The girdle of cilia is nothing but the first outline of the subsequent adoral zone, as the further course of the process shows. One can very easily recognise, close beside the girdle of cilia, a constriction which is at first shallow and easily overlooked, but which, after a short time, separates the two halves from one another, so that the connecting part is restricted to a small band. The two halves are easily recognisable as independent organisms, the more so since the granular inner substance is drawn back, especially posteriorly from the line of constriction. The arch of cilia has gathered more and more closely round the anterior pole of the posterior half, and has been continued inwards into a short, flat, but already triangular protuberance, formed close behind the extremity on the ventral surface. At this stage, the nucleus has usually divided into two parts, which lie one in each half, and are extremely like one another, especially since a second contractile vacuole has made its appearance. As the division progresses, the posterior peristomial region gradually acquires its more definitive structure, by the growth of the aforesaid protube-

rance, and the large cilia sink deeper into it, but finally persist in their former size only on the left margin. Sometimes one finds animals which are all but separate, being united only by a thin connecting thread. In one case in which I observed the separation, I saw this thread draw itself together into a ball, which remained connected with the anterior individual, and looked just like a little ball of dung which the animal was about to drop. These adherent balls are often seen in *Balantidium*, and have been quite generally described by previous investigators as dung-balls. That this is a mistake I have little doubt, not only because of the previous observation, but because of the fact that it is always the smaller and more slender forms with narrowed posterior extremity that bear this appendage. The size of this ball varies greatly, and is in some cases so considerable that Ekeckrantz regarded it as a bud, and was thereby led to the conclusion that these Infusorians also reproduced by budding. Although I have actually observed a small vacuole inside one of these balls, I am far from being inclined to interpret this occurrence according to Ekeckrantz's theory. The fact that budding occurs in but few groups of Infusoria, and has never yet been observed in forms allied to *Balantidium*, is of some weight in this connection. The same may be said in regard to the statement that it is the posterior end of the body which buds, for a terminal budding is, as far as we know, in the highest degree improbable among the Infusoria.

Division occurs, to all appearance, so frequently and rapidly among the Infusoria, that we can easily conceive how the number of parasitic inmates, after a time, considerably increases, and after a lengthened period becomes quite immeasurable. The parasitism itself cannot, of course, be thus explained.

The Mode of Infection by this parasite is at present in a state of uncertainty, and a decided proof is needed as to the form in which the *Balantidium* gains admission to its host, and until this is furnished our knowledge of the subject cannot claim to be satisfactory.

So far as we can judge from the analogy of other intestinal Infusoria, and especially from the facts lately established by Engelmann[1] and Zeller[2] as to *Opalina*, we may on *à priori* grounds expect that this transmission occurs in the encapsuled state, and therefore under circumstances which allow to the Infusorians a further distribution outside the living organism. And, as a matter of fact, it has been proved beyond a doubt that *Balantidium* has such an encapsuled state. Even in the first edition of this work I was able to state the results of some observations of this point, which were afterwards confirmed by Stein.[3]

[1] *Morphol. Jahrb.*, Bd. i., p. 573, 1876. [2] *Zeitschr. f. wiss. Zool.*, Bd. xxix., p. 352, 1877.

[3] Against this corroboration the negative results of Wising's observations have not much weight. Besides, Wising does not dispute the correctness of our statements, but

I may premise that *Balantidium* is by no means so sensitive to the influences of water and cold as the intestinal Monads. Even after copious application of water, we can, without using a warm stage, see the Infusorians moving for a long time without apparent diminution of vigour. But later the animals become wearied, they remain lying on the object glass, and finally suspend the play of their cilia. But even in this state they retain unchanged for hours a fresh appearance. One does indeed find some specimens which are already more or less strongly contracted, and have lost all their covering of cilia, except a few adoral ones. The granular interior mass has gathered together into a heap, from which some large drops of fat shine out. Later still, the cilia and the epistome have disappeared, and the body finally appears as a ball (0·08 to 0·1 mm.), which is surrounded on all sides by a capsule-like thickened cuticle, but still encloses as before a clearer peripheral layer and a dark central mass with fat-drops. The origin of the cyst admits of no doubt, for one can often observe in its earlier stages the nucleus and the vacuoles of *Balantidium.* Since this capsule is found in the deposited and even somewhat dry excrement, one may perhaps conclude that its formation as above described is an entirely normal process, occurring perhaps in all, and at least in many of the parasites expelled with the excrement. That the *Balantidium*-capsule plays an important part in the preservation and transference of these animals, is not only in itself most probable, but finds justification and confirmation in the facts known regarding *Opalina.* One may indeed doubt whether it is these encysted *Balantidia* exclusively which bring about the infection, or whether the newly voided animals are not sometimes directly transferred to the intestine, there again to become its denizens. So far as man is concerned, this question is indeed irrelevant, seeing it could hardly happen that he thus infected himself. But it is quite the reverse with swine, which, with their dung-eating habits, might easily afford opportunity for such a mode of infection.

In support of the position that an effective transmission is only brought about by means of the encysted animals, I lay but little emphasis on the fact that the attempts of Ekeckrantz and Wising to infect dogs and other mammals (*per os et per anum*) with dung containing *Balantidium,* have all yielded only a negative result; but I rely rather on the well-known fact that small delicate skinned Entozoa, as these forms undoubtedly are, cannot without a protective covering survive in the stomach of an animal (p. 76). And it is through the

thinks that one must not transfer the results of the observation of the *Balantidium* in swine to that found in man, and sees in this a further reason for not regarding man as the proper and natural host of this parasite.

stomach that the *Balantidia* must reach their destined habitation, for an entrance *per anum* is by the nature of the case impossible.

Man becomes infected with *Balantidium* by eating substances with which the encapsuled animals have come into contact; how this contact occurs we can hardly tell, it is simply the result of the same countless chances which determine the ubiquitous distribution of eggs of Helminths. Then, of course, the *Balantidium*-cysts are not imprisoned within the pig's dung, but if this be broken and dried up, they may be spread about without loss of the power of development, and may be conveyed to man with an ease proportionate to the closeness of the local relations obtaining between him and the swine.

As to the pathological import of *Balantidium*, we might answer much in the same words as in regard to the related Infusoria, the intestinal Monads, and the *Amœbæ*. It is uncertain whether they can be regarded as having actually a power of originating disease. Although they seem to be constant in pigs, no pathological phenomena result. Of course this is not decisive, for we know how different organisms are very variously affected by different influences; and it is perhaps worth noting, in connection with the above facts, that the excrement of pigs has usually a loose and stinking character, which is not normally the case in man.

But granted that we cannot directly affirm that the parasitism of *Balantidium* determines of itself a pathological state, it does not in the least follow that its presence is indifferent to its host. Rather it is, *à priori*, very probable that the movements of the animals, present as they are in thousands and hundreds of thousands, occasion a state of irritation which might easily increase and aggravate an existing disease. For this reason it is advisable, when the occurrence of this parasite has been proved, to take measures against it, as well as against any other disease.[1]

It is doubtful whether these parasites can live in a perfectly healthy intestine. Hitherto they have been found only in stools of patients otherwise diseased. If these changes be not regarded as a consequence of the parasitism, then evidently one must conclude that an abundant secretion of mucus (for the stools of infested persons are usually pulpy and diarrhœtic) is a condition favourable to the existence and reproduction of *Balantidium*, as, indeed, we have formerly concluded of the other intestinal Infusoria. But, on the other hand, it is doubtful whether we are warranted in ranking *Balantidium* among the so-called "putrefactive Infusoria," since they live more upon the fluid chyle than upon the secretions of the intestine.

[1] As to the means to be used (clysters of acetic and tannic acids), see especially the reports of Henschel's experiments (*loc. cit.*).

Sub-Kingdom II.—VERMES.

Bilaterally symmetrical animals without a skeleton, having a longer or shorter cylindrical or flattened body, which is either perfectly simple or exhibits a larger or smaller number of flat or ring-shaped segments, which thus give their possessors a certain resemblance to the Arthropoda. Dorsal and ventral surface often closely resemble one another. External appendages are in many cases completely wanting. When present, they consist either of organs of attachment (suckers, chitinous hooks, &c.), or, as in the majority of the segmented or ringed worms, of tufts of bristles, which are then distributed very regularly over the segments. Sometimes branchiæ are also found; if they be not present, the respiration is simply cutaneous. The habitat is in water or in damp localities; the motion is in general slow.

The animals now included under the designation *Vermes* form a group much more restricted than was originally intended by Linné in his famous "Systema Naturæ." The latter included under that name all the invertebrate animals, with the exception of the so-called Arthropods (*Insecta*, L.)—that is to say, a host of animals of the most heterogeneous types, which Cuvier first taught us to distinguish. Worms now include only a small group of these animals, namely, those which remain after the exclusion of the *Protozoa*, *Radiata*, and *Mollusca*.

To fix the natural limits and characteristics of this division is a very difficult problem of systematic zoology, especially difficult because the worms, even as now limited, represent no uniform group. For our present purpose it is sufficient to describe them as above.

In regard to internal organization, the worms exhibit almost greater contrasts than in external structure, for there is no single organ which is even essentially the same throughout. Not only is the body-cavity frequently wanting, so that the intestine and the cortical layer, otherwise separated by it, are united into a common mass, but in many cases neither blood nor blood-vessels are present. There are even a great many worms, and particularly among those which we are about to consider, which are entirely destitute of an alimentary canal, although this is by far the most constant of all animal organs, and is hardly ever wanting in the other Metazoa. The disposition of the muscular and nervous systems also exhibits numerous and important differences, which are partly co-ordinated with the external structure of the body. The only organ constantly present is an

anterior so-called cephalic ganglion or brain, from whieh the nerves radiate anteriorly and posteriorly. In the segmented forms the branehes running back are united into a single ventral eord, whieh forms a speeial nerve ganglion in eaeh segment. The sexual organs exhibit, in the flat-worms at least, a very eonsiderable development. They eonsist of male and female parts, which are sometimes in separate individuals, but are also often, and perhaps more frequently, united in the same body.

The development is as a rule associated with a metamorphosis. In many groups there is an alternation of generations. Thus we distinguish the so-called "nurses," whieh arise directly from the eggs, and the "sexual animals," whieh originate partly by budding, and partly from egg-like eells in the interior of the "nurses."

Of all the divisions of the animal kingdom, that formed by the worms is by far the most important for our present purpose, for to it belong the great majority of parasites, and these the most dangerous.

In man the parasitic worms inhabit exelusively the internal organs, where they are soaked by the juices of their host. Only on aquatie animals do we find them as external parasites. Their eetoparasitism on land animals is rendered impossible by the necessary conditions of respiration (see p. 13).

The parasitic worms infesting man and the higher animals are therefore literally intestinal worms (Entozoa). They have a true right to this name, which is often used in a wider sense to denote all parasitie worms, including even ectoparasites.

At one time these worms were regarded as forming a single united group, not only with a biologieal, but also with a systematic signifieance; in other words, they were erected into a special class of Entozoa or Helminths. So is it aeeording to Cuvier, for example, and also aeeording to many more modern zoologists—*e.g.*, Owen, v. Siebold, van der Hoeven, &c. Cuvier even had the idea of separating this class of Entozoa from the worms proper (*i.e.*, from the ringed worms (Annelida), which he had united with the likewise ringed Arthropoda into a single group, Annulata), and thought of uniting them with the Radiata.

Now, however, zoologists are of a different opinion on this point. Not only do they insist on the union of the Helminths with the higher worms, but deny the propriety of a special class of intestinal worms in any natural system of the animal kingdom.

Even the adherents of the older opinion must at any rate confess that the aforesaid class "includes most diverse animals"—so diverse, indeed, that no common eharacter in their organization is to be found. In reality the limits of the class are simply those of a common mode

of life,—a characteristic very important from a biological point of view, but only of subordinate importance in determining natural relationship. To base a classification on such physiological characters is in this case all the more illegitimate, since we know that not a few Helminths live for a longer or shorter part of their life in freedom.

Also, the older zoologists have never scrupled to refer certain non-parasitic forms, such as the *Rhabditis* (*Anguillula*), to this group, and to refer other really parasitic worms, such as *Chætogaster*, *Hirudo*, &c., to their place beside the true worms.

When we further recall how many Helminths have an undeniable relationship with free-living worms—how the Trematodes, for example, are, as we have seen (p. 105), closely allied to the Turbellaria—how the leech comes almost as a connecting link between the Helminths and the higher worms—we shall be sufficiently convinced of the truth of the opinion staunchly upheld half a century ago by my uncle, F. S. Leuckart[1]—namely, that a class of Helminths has only the rank and import of a faunistic group, and ought never to be invested with a systematic unity.

Since the time of Zeder and Rudolphi five distinct groups of Helminths have been generally recognised, whether unified into a special class or no—viz., the thread-worms or Nematodes, the Acanthocephali, the flukes or Trematodes, the tape-worms or Cestodes, and the bladder-worms or Cystici. The attempt of Diesing to form a sixth order—*Acanthotheci*—of the so-called Pentostomata has only found a limited support, and calls for no further notice, since we are decidedly convinced (p. 14) that these animals, in spite of a certain superficial resemblance to Helminths, have no more claim to be classed as worms than have the Lernæadæ (p. 92), which were referred to the same class before v. Nordmann's investigations. Just as the latter are Crustacea, as their larval stages indisputably prove, so are the former to be regarded as peculiarly modified mites.

Nor has it been possible for the five orders of Rudolphi to remain unaltered, for experimental helminthology has established beyond doubt the opinion of Dujardin, v. Siebold, van Beneden, and others, that the bladder-worms were no independent species, but only stages in the development of Cestodes. The order has thus vanished from systematic zoology, and the number of groups of Helminths is thus reduced to four, which have, according to all results, a reasonable claim to be regarded as natural divisions.

On closer inspection, however, it soon appears that they are not equally closely united to one another. As we formerly showed

[1] "Versuch einer naturgemässen Eintheilung der Helminthen, nebst dem Entwurfe einer Verwandschafts- und Stufenfolge der Thiere überhaupt:" Heidelberg, 1827.

(pp. 105-109), the Cestodes are closely united to the Trematodes, and the Acanthocephali to the Nematodes; and this is not only a superficial resemblance, but concerns the development and the anatomical arrangement of the intestinal organs. In certain cases the resemblance is so great that it is difficult to determine with certainty the systematic position of the animal. Thus we know of Helminths which seem intermediate types between Cestodes and Trematodes — such as *Amphiptyches* and *Amphiline.* The connecting links between Nematoda and Acanthocephali, though not so perfect, are not wholly wanting (*Gordius*).

Thus we can distinguish two great groups of Helminths which have been named according to their most conspicuous external characteristic respectively—*Playthelminthes* (*Platyhelmia*) and *Nemathelminthes* (*Nemathelmia*).

We must not, however, forget that these two groups do not represent definite unities, any more than do the Entozoa or Helminths. The intestinal worms have originated, as we have shown (p. 89 *et seq.*), by the adaptation of originally free-living forms to a parasitic environment, and both groups are in various ways connected with free-living relatives. The natural system has attempted to express this relation by associating the Platyhelminthes with the Turbellaria and Hirudinea, and Nemathelminthes with the other free-living worms; in other words, by distinguishing two classes of worms, which include both free and parasitic species, and which are not unfitly distinguished by their characteristic forms as flat-worms (*Platodes*) and round-worms (*Annelides*). I will indeed grant that there may be a difference of opinion as to the limits, and even justifiability, of these two classes. This is especially so in regard to the second class, which includes forms widely differing from one another—besides the Nemathelminthes and *Chætognathi* (*Sagitta*), also the *Gephyrea* and *Chætopoda.* The position of the Hirudinea among the flat-worms has also become doubtful (p. 107).

But all these are questions of subordinate importance for us here. We have to discuss not the systematic position of worms, but their structure and life-history. The above remarks will serve as a general introduction as to the relations of these forms.

Class I.—PLATODES.

Schneider, "Untersuchungen über Plathelminthen," *Vierzehnter Bericht der oberhess Gesellsch. für Natur- u. Heilkunde:* Giessen, 1873.

Minot, "Studien an Turbellarien, Beiträge zur Kentniss der Plathelminthen," *Arbeiten des zool.-zoot. Institutes in Würzburg*, Bd. iii., 1876-77.

Animals with a more or less flat and short body, seldom ringed, either with no appendages, or with organs of attachment in the form of suckers and hooks, varying in number and arrangement. In a few cases there are gills. Generally hermaphrodite, the young forms sometimes resemble the adults, but sometimes differ from them, and exhibit an alternation of generations before attaining sexual maturity. When this takes place by budding, the sexual animals remain for a long time united with their nurse in a polymorphic colony.

The majority are temporary or stationary parasites, as the frequent occurrence of fixing organs would lead one to suppose.

The alimentary canal has a fleshy pharynx, discharging the function of an organ of attachment or of capture, and showing, in accordance with the form of the body, a striking tendency to ramification. In many cases the anus is absent, in others (endoparasites) even the whole canal, so that the ingestion of food takes place by the surface of the body. Blood and blood-vessels are only found in segmented flat-worms. They have indeed been described also in other forms, but this was due to a confusion with an often ramifying excretory apparatus which generally occurs in these organisms. The nervous system consists of a ganglion lying in front of the mouth-opening, or at the anterior end of the body, and of nerves running from this, usually with two specially strong and well developed lateral branches. In the segmented flat-worms these unite in the middle line, and form a single chain of ganglia running below the alimentary canal. The sense organs are usually but slightly developed, and in the endoparasites are generally present only as tactile organs.

A body-cavity, usually present to contain the vegetative organs, is here wanting. These animals are parenchymatous worms (*vers parenchymateux*), *i.e.*, organisms whose viscera are in continuity with the other tissues, and are directly embedded in the general connective, tissue substance of the body like the muscles and nerves. In other words, the splitting which usually separates the mesoderm into an outer somatic and an inner splanchnic layer has not taken place, or if,

as in the Hirudinea, it has existed for a time, it has been obliterated in the course of further development. Under such circumstances the musculature of the viscera only rarely acquires any independence, and is generally closely connected with the musculature of the body. However, this is not equally true, as we shall presently see, for all Platodes. Nor is the disappearance of the body-cavity always quite complete, for some of the higher, and even some of the lower (parasitic) forms show evident traces of this structure.

Order I.—CESTODA.

Van Beneden, "Les vers Cestodes ou Acotyles," *Mém. Acad. roy. Belg.*, t. xxv.: Bruxelles, 1850.

Idem, "Mémoire sur les Vers intestinaux," p. 112: Paris, 1858.

Flat-worms without mouth or alimentary canal, which typically develop by alternation of generations, by budding from a generally pear-shaped nurse, with which they remain united for a lengthened period as a ribbon-like colony or "strobila." The individual joints of the colony, i.e., *the sexual animals or Proglottides, increase in size and maturity as they are removed further from their origin, by the intercalation of new buds, but are not distinguished in any special way. The nurse, however, known by the name of the "head" (Scolex), is provided with four or two suckers, and usually with curved claw-like hooks. The dorsal and ventral surfaces of the head are perfectly identical, so that the arrangement of the hooks presents a strikingly radiate appearance. By means of this apparatus the worms fasten themselves on the intestinal membrane of their hosts, which (except in the case of the otherwise peculiar* Archigetes) *all belong to the vertebrates. The nurses develop in a more or less complicated fashion as so-called "bladder-worms" from little round six-hooked embryos. The latter inhabit very diverse but usually parenchymatous organs of the higher and lower animals, and are thence passively transferred to the intestine of their subsequent host.*

What we have here described as a polymorphic colony is that creature which is commonly called a "tape-worm," and regarded as a simple individual with a head and jointed body. At first sight this common conception seems to be perfectly justified, but it can hardly be upheld in face of the facts of the case. It is, for instance, scarcely consistent with our idea of an individual animal to observe that not only can the terminal "ripe" joints of the tape-worm separate themselves with the greatest facility, and creep about for a while as inde-

pendent animals,[1] but the so-called head can, after the loss of its chain of joints, grow again to a new tape-worm within a few weeks. Can we wonder that these observations long ago raised a doubt as to the correctness of the usually accepted theory, and that thoughtful

FIG. 131.

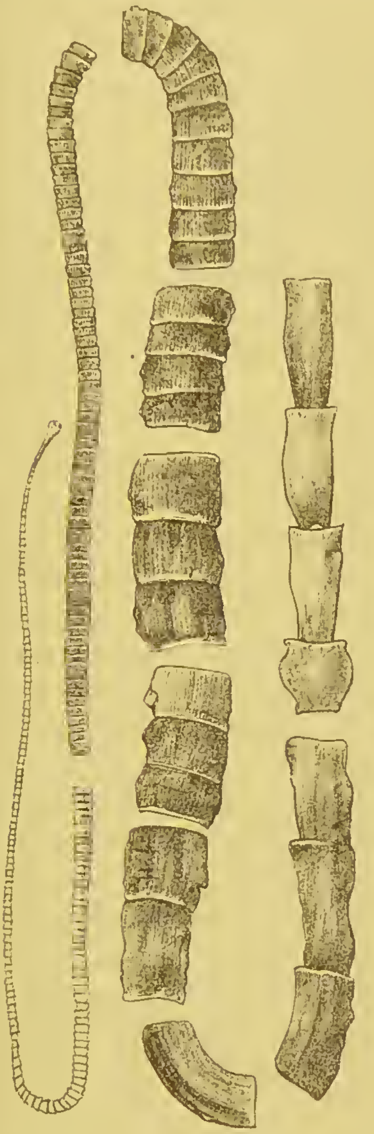


FIG. 132.

FIG. 131.—Tape-worm form of *Tænia saginata s. mediocanellata.*

FIG. 132.—Isolated Proglottides of the same.

investigators more than a century ago suggested that the tape-worm was no simple individual, but a compound animal.

Not to speak of the Arabian physicians, this was the opinion of Vallisnieri[2] and Coulet,[3] and also of Linné, who places the tape-worm

[1] In fact, these discharged joints, especially of *Tænia saginata*, have been repeatedly considered both in ancient and modern times as distinct parasites, *Vermes cucurbitini.*

[2] "Considerazioni ed esperienze intorno alla generazione dei vermi del corpo umano," p. 75 : Padova, 1710.

[3] "Tractatus de ascaridibus et lumbrico lato," p. 37, &c. : Lugd. Bat., 1729.

in his system beside the polypes among the polyzootic zoophytes, and in other places[1] expressly compares it with a plant of many shoots.[2]

Linné's conception was also in advance of his contemporaries in this respect, that hitherto they had been inclined to suppose that the tape-worm arose by the isolated joints (*Vermes cucurbitini* = *chabb al-kar'i* of the Arabians) subsequently forming a chain. And this idea struck its roots so deeply that even Blumenbach, towards the end of last century, regarded it as correct. Even the unequal development of the individual joints, which surely suggests successive budding, did not lead him to alter his opinion. He tried, indeed, to explain it by assuming that the older worms were ever being sucked out by their progeny, and were thus reduced in size. And yet even at this time the observations of Pallas and others had made it almost indubitable that the smaller joints were the younger, and that they attained the larger size as they gradually grew older.

The conception of the tape-worm as a polyzootic animal could, however, only slowly gain ground. It appeared as though the presence of a distinct and definitely formed head could not be brought into harmony with it. Pallas, following up Linné, had indeed already attempted to regard this head as the root (quasi-radix) of a plant-like animal, yet, with the exception of Reimarus, but few zoologists supported his idea. And so it has come about that, in spite of the protests of F. S. Leuckart and Eschricht, the tape-worm has even in our own day, in scientific and popular conception, been persistently regarded as a simple animal.

It persisted in fact till Steenstrup[3] gave us the key to the proper understanding of the tape-worm, by showing its harmony with his theory of alternation of generations, according to which the head was seen to be the larval "nurse," and the joints the sexually mature individuals. The ingenious Danish naturalist left us, indeed, without a strict proof of the correctness of his theory, but this was speedily furnished in such masterly fashion by van Beneden[4] and v. Siebold,[5] that it is now hardly permissible to harbour a doubt as to the compound character of these animals.

[1] "Amœnit. acad.," vol. ii., p. 87 *et seq.* (Dissert. de tænia).

[2] *Götting. gelehrt. Anzeig.*, No. 154, 1774.

[3] "Generationswechsel," p. 115: Kopenhagen, 1841; "Alternation of Generations," Ray Society, 1845.

[4] "Les vers cestoides sont-ils mono- ou polyzoiques?" "Vers Cestoides," p. 94, and "Mém. sur les vers intest.," p. 251.

[5] "Ueber den Generationswechsel der Cestoden:" *Zeitschr. f. wiss. Zool.*, Bd. ii., p. 198, 1850. See also his "Abhandlung über Band- u. Blasenwürmer," 1854.

As the often corroborated observations of these investigators showed, there is in the developmental history of the Cestodes a stage in which nothing of the future tape-worm is to be seen, except the so-called "head," which then lives by itself like an independent animal, and only gradually and under favourable conditions buds out one joint after another from its posterior extremity. This isolated tape-worm head, or more correctly "nurse," had indeed been formerly observed, but its true value was not detected, and it was usually regarded as the representative of a special form (*Scolex*, &c.).

FIG. 133.—Isolated living "head" of *Echinobothrium minimum*, van Beneden, from the intestine of *Trygon pastinaca*.

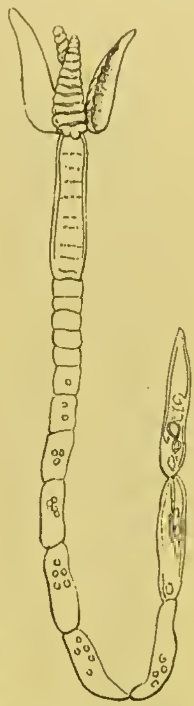


FIG. 134.—Chain of joints of *Echinobothrium minimum*.

The joints, which are budded off one after the other, are like all buds, at first small and immature, but they gradually increase in size and maturity as they are pushed further from the head by the intercalation of new buds. After a certain time, or, what comes to the same thing, at a certain distance from their nurse, they become sexually mature, sooner in some species than in others. The head, which is usually designated by the originally much more restricted name of "Scolex," remains, like a true nurse, asexual.

Thus by continued budding there arises from an originally isolated nurse a whole community of individuals—a colony, in which one has to distinguish not only animals at various stages of maturity, but also one asexual and aberrant member, the so-called "head."[1]

The significance of this head is not, however, purely genetic. It is not only the origin of the whole chain, but serves further for its fixation, and thus benefits the whole colony. It was formerly believed that nutrition was also effected by the head;[2] the suckers were regarded as mouth openings (Nitzsch, Owen), or the oral opening was

[1] Van Beneden used the term "strobila" to designate this colony. It was formerly employed by the famous Norwegian zoologist, M. Sars, to denote a stage in the development of certain jelly-fish (*Aurelia*)—a stage, indeed, formerly described by him as a new species. In this instance we have, as in the tape-worm, a "nurse" here in the form of a polype, on which there rises a pillar of young jelly-fish, at first imperfectly separated from one another, but afterwards set free. See *Archiv f. Naturgesch.*, p. 9, tab. i., 1841.

[2] As we shall afterwards see, a similar opinion has lately been advanced by Blumberg.

looked for between the suckers (Bremser, Mehlis), at a point on the top of the head, where the outer coverings are often drawn together into a depression, and where, in some species, a minute but distinct sucker (the frontal sucker) is formed. We know, however, that the Cestodes are wholly destitute of both mouth and alimentary canal. The observation of two repeatedly described longitudinal channels suggested the existence of an alimentary canal, and therefore lent some probability to the above belief in the presence of a mouth, but we shall afterwards see that they are only the main stems of the so-called "excretory vascular" system.

The physiological significance of the head referred to above is evidently important, since the suspended sexual animals are destitute of hooks. The nurse undertakes the attachment of the colony, and thus has its specific share in the general economy, as is usual in cases of polymorphism.[1]

The association of sexual members (the so-called "Proglottides") is not, however, a lasting one. Sooner or later the terminal joints become loose, sometimes singly, sometimes in groups, and after remaining for a while in independent freedom beside their still attached fellows, are carried along with the fæces from their intestinal home. As a rule, this separation takes place only after the perfect development of the discharged sexual members, and often, as in *Tænia*, after even their embryos are mature;[2] but there are cases where the joints are liberated much earlier. Thus, thanks to van Beneden, we know of certain forms from the alimentary canal of the predatory rays and sharks, whose proglottides only reach maturity after they have become free, and which, in their isolated state, grow to a size almost as great as that of the whole tape-worm, from which they originated. With such cases before us, every doubt as to the independent nature of the individual joints must vanish.

Fig. 135.

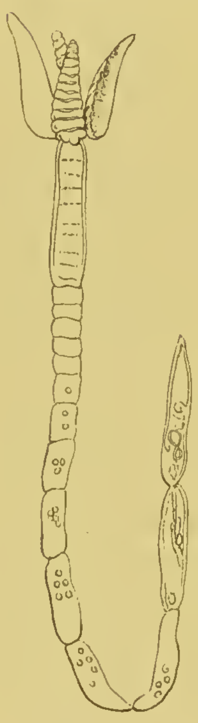


Fig. 136.

Figs. 135 and 136.—Strobila and Proglottis of *Echinecibothrium minimum* (after van Beneden).

[1] See Leuckart, "Ueber den Polymorphismus der Individuen oder die Erscheinungen der Arbeitstheilung in der organischen Natur:" Giessen, 1852.

[2] Hence the name "*Ovaria ambulantia*," sometimes applied by Pallas to the sexual animals of *Tænia*.

We would not, however, conceal that there are, on the other hand, certain tape-worms in which the sexual animals are never isolated, and some indeed in which the jointing is so incomplete that only an indistinct constriction (*Triænophorus*) or merely successive sets of generative organs (*Ligula*) suggest the composite nature of the body. If we compare this state of matters with what we find in other composite animals, we shall not be led into error; it only proves that the independence of the united individuals, or, if one prefer it, the individualisation of the joints, is of different degrees in different cases.

Even the external characteristics of the tape-worms give us some standard in judging of these degrees of individualisation. The earlier and the more sharply the individual joints are marked off from one another, and the looser their mutual association, the greater will be their independence in a biological sense. And thus it is the typical forms of *Tænia*, with their narrow joints, like the seed of a melon (Fig. 131), which most evidently exhibit the polyzootic nature of these animals. The joints separate singly, and then in their movements and behaviour appear as perfect, independent individuals. In the broad, short joints of the *Bothriocephali* (Fig. 137), this independence is not so marked, for they are liberated, not singly, but in groups of varying number. In the unjointed forms there is, of course, no regular liberation. The individual parts are here subordinated to the whole, both anatomically and biologically.

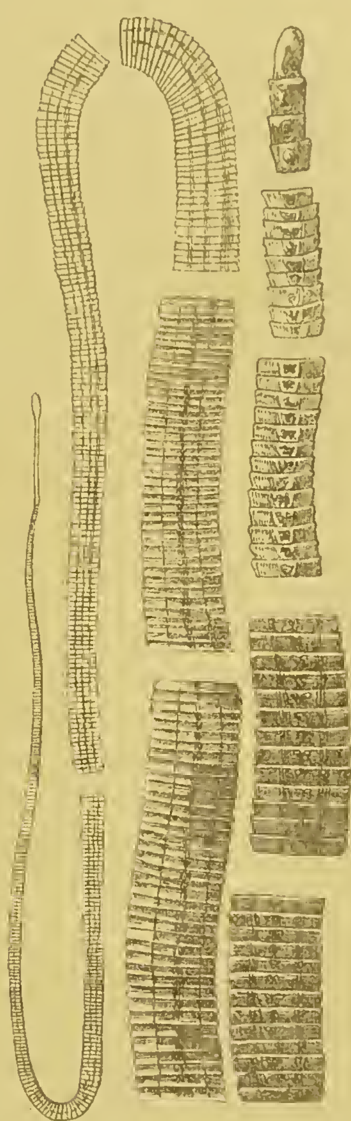


FIG. 137.—*Bothriocephalus latus.*

The forms hitherto mentioned do not, indeed, represent the highest degree of centralisation possible to the Cestodes, for there are tape-worms, as has been previously pointed out (p. 106), where the body is destitute of any kind of joint. There is a short proglottis—like a flat-worm—which contains only a simple generative organ, and is

provided anteriorly with a more or less highly developed apparatus of hooks (*Caryophyllæus, Amphiptyches*). In such cases there is no distinction between nurse and sexual animal, or head and joint; the life-history, which is in ordinary cases spread over two generations, is here perfected in the same individual; instead of alternation of generations a simple metamorphosis is seen.

Physiologically, the polyzootic tape-worm is a composite colony. Sensation and movement, nutrition and excretion, are distributed uniformly over all the joints, as if they were simply organs of one individual and were not themselves individualised. In respect of their functions they are, indeed, like organs, or "parts of a higher unity," but the unity which they form and uphold by their combined effort is, morphologically, not a single individual but a colony.

It was obviously these indications of a physiological unity which hampered the true conception of the structure of the Cestode, and ever recalled the old opinion that the tape-worm, even in its joitned form, was a single animal. It was seen that the movements passed as waves from one joint to another, that considerable portions of the worm could extend their length, or, by contracting, increase their breadth. How was this possible, except on the supposition of a common and single impulse? A number of canals were seen running continuously throughout the chain; did not this prove the individual simplicity of the body? Was it not, after all, more natural that the nurse should be regarded as the "head," and the divisions filled with eggs as the "joints?"

The physiological unity of a polymorphic community is not less wonderful now than it ever was, but we have gradually become accustomed to it. We see the same thing in every case where similar conditions obtain.[1] Could one doubt that the bees of a hive form a colony in spite of their separateness and various kinds, or that the operations of the indisputably distinct individuals of such a colony are not as mutually complemental and co-operative as if they were directed by an individual will?

But no more need be said in favour of a theory which is sufficiently justified by the facts of development.

We have to distinguish, then, in the so-called "tape-worm" two kinds of individuals—the "head," originating the whole colony (the "root" of Pallas, the "bulb" of Reimarus), and the subsequently produced "joints." At the first glance the latter differ markedly from one another, the anterior joints near the head (the "neck") being small, and often indistinctly separated; but all the

[1] See my treatise on Polymorphism, referred to above.

differences are simply dependent on age and development. The anterior joints are the youngest, and therefore smaller and more immature than the posterior, which have gradually attained their full size and maturity. The chain furnishes us with a perfect succession of developmental stages, and consists sometimes of many hundred joints, though sometimes of only a few,—in *Tænia echinococcus* of three or four (Fig. 138).

Fig. 138. Adult specimen of *Tænia echinococcus.* (× 12.)

The differences between head and joints are, mainly, that the former is provided with suckers and hooks, and that the latter enclose highly developed hermaphrodite reproductive organs. But besides this characteristic and essential difference, there are many minor ones, so that in fact hardly any common character can be mentioned. It would be difficult to recognise a flat-worm in the head, since it is usually pear- or club-shaped, and from the perfect similarity of the dorsal and ventral surface, conforms rather to a radiate than to a bilateral type. This is most decidedly seen in the *Tæniæ*, where the head (Fig. 139) is not only constantly provided with four suckers, arranged two on either side round the longitudinal axis, but bears also a neat circle of hooks on the apex, which conform exactly to the architectural relations of the radiate animals, both in their high number and regular arrangement. The interior organs also, and especially the excretory vessels, show a distinct radiate arrangement. In other cases the radiate structure is certainly less striking; for not only do the hooks often lose their circular arrangement, and form groups corresponding in number and position to the four suckers, or even wholly disappear, but even the structure of the suckers changes. Sometimes the four approximate in pairs, and fuse into two more or less simple suckers, thus assuming a bilateral arrangement; or, instead of the lateral suckers, two median ones appear, one on the dorsal and one on the ventral surface, as in the genus *Bothriocephalus* (Fig. 140).

In contrast to this formation of the head, the sexual animals possess an undeniable bilateral structure. This is, however, not always shown with equal clearness and emphasis; indeed, the lateral symmetry is often disturbed, as also not unfrequently happens in other bilateral animals. But it is only the generative organs which are thus asymmetrical, the others lie on either hand in exactly the same fashion. And sometimes even the generative apparatus is quite symmetrical, as, for example, in the genus *Bothriocephalus*, whose sexual animals are in a certain sense typical Cestodes. The genital

ducts and openings lie (Fig. 141) in the middle line, and are so arranged that the openings are on that surface towards which the

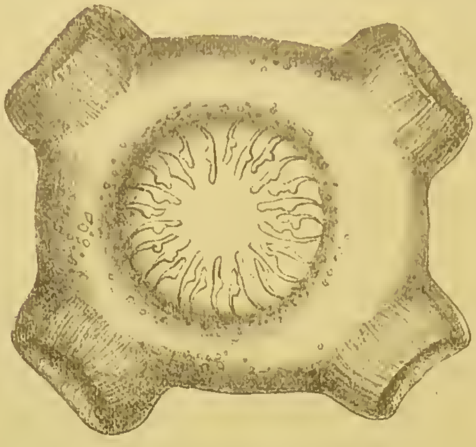


Fig. 139.—Apex and hooks of *Tænia solium.*

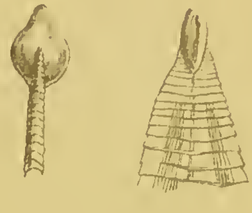


Fig. 140.—Head and anterior portion of *Bothriocephalus cordatus.*

female ducts are approximated, while the male organs lie near to the opposite surface. According to the analogy of the Trematodes, the former must be the ventral surface, and the latter the dorsal; and among the Tæniadæ also there are forms which exhibit like conditions, as, for example, the *Tænia litterata* of the fox. As a rule, however, the genital openings are shifted from the middle to the side walls,

Fig. 141.—Generative organs of *Bothriocephalus latus* (ventral aspect).

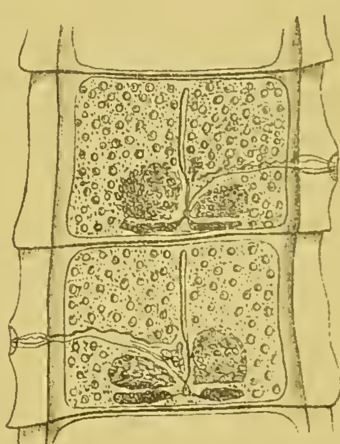


Fig. 142.—Generative organs of *Tænia solium.*

and are found either all on one side, or on either side in an irregular alternation (Fig. 142.) In such cases it would be hardly possible to distinguish the dorsal and ventral surfaces, were it not that the

position of the generative organs—*e.g.*, of the testes dorsally—affords us certain fixed points for their determination.[1]

As we shall afterwards see, there are also Trematodes with marginal genital openings, but their number is so small that this position of the openings must be regarded only as exceptional, while in the case of the Cestodes it is almost the general rule even outside the group of the Tæniadæ. On *à priori* grounds one would expect these peripheral openings to occur on either side, but there are only few species in which this is the case—(*Tænia elliptica*, *Tænia expansa*, &c., Fig. 143). In spite of this, it must be regarded as forming the basis of the common asymmetrical formation, and this is proved by certain individual variations, which we shall have further occasion to discuss particularly. Thus one finds, for example, joints of *Tænia solium* with symmetrical marginal pores, and joints of *T. elliptica* occasionally asymmetrical. In bilateral animals, the unpaired mesial organs are, as is well known, very often represented by two lateral symmetrical organs. If further proof be needed of the morphological identity of the lateral organs in *Tænia* with the median structures of *Bothriocephalus*, this might be noted, that in some species of *Bothriocephalus* (*B. fasciatus*, *B. tetrapterus*), the genital openings lie, not, indeed, exactly marginally, but regularly, right and left of the middle line. And while this occurs here as a rule, it also appears as an exception in other species.

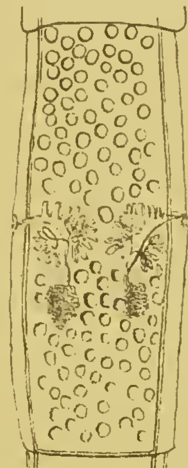


FIG. 143.—Sexually mature proglottis of *T. elliptica*.

The Anatomy of Cestodes.

Sommer and Landois, "Ueber den Bau der geschlechtsreifen Glieder von Bothriocephalus," *Zeitschr. f. wiss. Zool.*, Bd. xxii., pp. 40-100, 1872.

Schiefferdecker, "Beiträge zur Kenntniss des feinern Baues der Tänien," *Jenaische Zeitschr.*, Bd. viii., pp. 459-488, 1874.

Steudener, "Untersuchungen über den feinern Bau der Cestoden," *Abhandl. d. naturf. Gesellsch. zu Halle*, Bd. xiii., pp. 277-366, 1877.

Kahane, "Taenia perfoliata, als Beitrag zur Anatomie und Histologie der Cestoden," *Zeitschr. f. wiss. Zool.*, Bd. xxxiv., p. 175, 1880.

[1] In the first edition of this work I called attention to the peculiar distribution of the generative organs of *Tæniæ*, and indeed of Cestodes generally. My conclusions have since been corroborated, especially by Kahane (*Zeitschr. f. wiss. Zool.*, Bd. xxxiv., p. 214, 1880), and by Moniez (*Bullet. scientif. dép. du Nord*, p. 220, 1878), who has, indeed, failed to notice my previous observations on the subject.

In our general discussion of the flat-worms we have already noted that the Cestodes are parenchymatous animals. The whole body is one mass, the continuity of the tissues is not broken by any visceral cavity. The vegetative organs are embedded in the general substance just like muscles or nerves.

The simplest and most convincing proof of this is furnished by their longitudinal and transverse sections, which are easily cut from carefully hardened specimens, and which, with the help of the now familiar staining and clarifying reagents, show the structure of the organism most beautifully.[1]

The Body-Parenchyma.—The mass of the Cestode body is in its morphological and histological relations a hyaline connective tissue of varying firmness, and developed so abundantly that one can almost fancy that the whole body of the animal has been modelled out of it. Externally, it is surrounded by a cuticle which is elevated at many points, especially on the head, into little spikes and hooks. The interior of the body, apart from the viscera, is traversed by muscular fibres, which run sometimes singly, sometimes in bundles, and generally in all three dimensions of space, so that the body-mass can be contracted on all sides. The more conspicuous are the longitudinal and transverse fibres, which at some distance from the exterior are developed in such numbers, and so close to one another, that the whole body-parenchyma is thus divided into two successive outer and inner sheaths, which (following Eschricht) we will respectively designate as "cortical layer" and "middle layer."[2]

The middle layer is seen on cross section to be bounded externally by a narrow clear border[3] (the strong muscular bands), and includes the generative organs, the longitudinal vessels, and the nerve cords; while the cortical layer mainly consists of the numerous muscular fibres, and a considerable number of round, solid, laminated concretions—the so-called "calcareous bodies"—which contain a considerable but varying proportion of lime salts.

[1] I need hardly mention that such methods were but little known or practised when the first edition of this work appeared (1862). So far as I know, I was the first to apply them to the investigation of Helminths, or indeed of Invertebrata in general. I mention this not to claim credit for it, but as an excuse for the errors which crept into my former account, largely in consequence of my necessarily imperfect methods.

[2] The latter includes the "transparent" layer distinguished by Eschricht in *Bothriocephalus latus*, and also the so-called ventral and dorsal granular layers. See *Nova Acta Acad. Cæs. Leop.-Carol.*, t. xix., Suppl. 2, 1841.

[3] Pagenstecher believes (*Zeitschr. f. wiss. Zool.*, Bd. xxx., p. 177, 1878) that he can distinguish a narrow space within the muscular layers of *Tænia critica*. This he would represent as a body-cavity. I have never seen any such appearance in my examination of numerous species.

They are not, however, exclusively confined to the cortical sheath, but are also to be found in the middle layer, only sparsely, however, in the mature joints, though indeed in considerable numbers before the development of the sexual organs. We must also note that their number varies not only in individual cases but in the different species, and this to such an extent that one sometimes looks for them almost in vain, while in other cases they are present in extraordinary abundance.

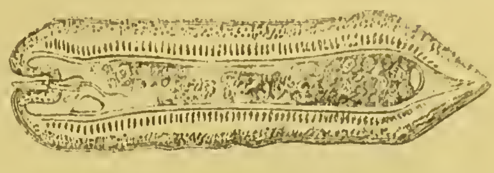


FIG. 144.—Cross section of *Tænia solium*, showing middle and cortical layers, under low power.

In the Bothriadæ, as we shall afterwards see, the cortical layer also includes the numerous cell-groups which form the yolk-glands (Eschricht's ventral and dorsal granules).

The connective tissue nature of the ground substance has been recognised on all hands since the publication of my researches in the first edition of this work. Opinions differ, however, as to its exact histological structure. I still maintain that it partakes of the nature of cellular connective tissue. The cells are indeed seldom provided with a distinct cell membrane, in fact they are usually mere nucleated masses of clear protoplasm, and sometimes (especially in the ripe joints) are fused together into a mass, leaving only their nuclei distinct. But these characters not unfrequently occur in connective tissue. In other cases one can observe a distinct intercellular substance usually in the form of a tolerably well-defined cubical network of bands and fibres, with cells of various sizes (up to 0·01 mm.) lying in the meshes. Here and there the nuclei are so closely appressed to the intercellular substance that one can easily mistake the fibres for processes of special cells. There are, indeed, in the parenchyma of the Cestodes true fibre-like cells, some spindle-shaped, some multipolar, the former lying in the so-called subcuticular sheath, as we shall afterwards have occasion to notice. The multipolar cells, which have been hitherto noticed only by Schiefferdecker, possess a membraneless, finely granular protoplasm, enclosing a very distinct nucleus, and running out into a varying number of long, thin, sometimes even reticulated processes of a similarly finely granular nature. They are found scattered through the whole parenchyma, especially in large *Tæniæ*, and sometimes recall ganglion cells.

The Calcareous Bodies.—We have already noticed these as distributed through the body-parenchyma, and belonging specially to the cortical layer. These concretions vary in size up to 0·019 mm., and have a

generally spheroidal, but often elliptical or kidney-like shape. In their solidity, in their power of refraction, and above all in their more or less distinct concentric lamination, they remind one of starch grains. Sometimes the central mass is distinguishable like a nucleus from the surrounding substance, which is occasionally radiately arranged. In some cases the bodies form twins, with two or three centres and an irregular form.

FIG. 145. — Calcareous corpuscles of *Tænia serrata*, showing various forms and sizes.

Very varied opinions have been held as to the nature of these calcareous bodies since they were first described by Pallas and Göze. In the bladder-worms, where they often occur in most extraordinary abundance, they were frequently regarded as eggs, or as blood and lymph corpuscles. It was only after the lapse of some time that Doyère and others proved that they were mainly composed of carbonate of lime. This altered the nature of the current explanations, and v. Siebold, reasoning on the analogy of similar bodies in the lower animals, claimed them as skeletal, while Claparède thought they were the results of an execretion.[1] This opinion was based on an observation made in the first instance on a Trematode-larva, but which seemed to shed a new light on the nature of these bodies in the Cestodes. Claparède thought he had clearly established that these structures were not freely embedded in the body-parenchyma, but were surrounded by pouch-like dilatations of the terminal branches of the excretory system. Although I formerly believed myself warranted in confirming these conclusions from an investigation of an oceanic Cestode[2] (the *Echinobothrium* of the ray), which I conducted along with Pagenstecher, and indeed attempted in the first edition of this work to support the above theory, and to remove the physiological arguments against it, yet I feel myself now compelled, along with other investigators (Rindfleisch, Landois and Sommer, Schiefferdecker), to adopt v. Siebold's opinion. I must, however, leave it undecided whether these bodies have any other functional significance than as supporting or protective structures.

It would, however, be a mistake to suppose that the designation "calcareous bodies" implied that these structures were wholly composed of lime. In the tape-worms they do indeed contain in many cases a very large proportion of lime[3]—21 per cent. of salts (mostly

[1] *Zeitschr. f. wiss. Zool.*, Bd. ix., p. 99, 1858.

[2] "Untersuchungen über niedere Seethiere," *Müller's Archiv f. Anat. u. Physiol.*, p. 605, 1858.

[3] There are, besides, small quantities of magnesia, oxide of iron, soda, and potash.

calcium salts) in the case of a newly examined *Tænia marginata*, according to an analysis made at my request by Professor Naumann in Giessen. But the most superficial micro-chemical examination reveals in the calcareous bodies the presence of an organic mass which is associated with the lime, and which can even be isolated as a clear ball of the original size by dissolving out the lime with an acid. Since this process is accompanied with more or less effervescence, the lime is therefore, for the most part, though we cannot say exclusively, deposited as carbonate of lime.

In some cases the bodies do not effervesce on being treated with acid, and this even in some species where they have previously been observed to do so. I tried formerly to explain this fact by the supposition that the carbonate had been replaced by some other salt of lime, but I have been informed by Sommer and Landois that small quantities of carbonic acid gas, instead of escaping in bubbles, are absorbed *in statu nascente* by the surrounding fluid, and that thus the absence of effervescence is in no way a sign of a complete absence of carbonic acid gas.

That effervescence should be absent when the calcareous bodies are present in smaller numbers, seems to me hardly to explain why it should be absent under certain circumstances in forms which usually exhibit it. Nor is the development of gas observed in all the corpuscles in equal intensity. Since they also differ markedly in appearance, lustre, and power of refracting light, I think we may assume that not only the number, but the composition of these calcareous bodies, is subject to manifold individual and specific variations.

It appears to me a mistake to regard the calcareous bodies of the Cestodes as unalterable and permanent structures. As they arise and increase during the development of the joints, so they under some circumstances decay. This is most easily observed in species where they are numerous. Thus *Tænia serrata* is not only much more richly provided with them in its cysticercoid stage than later, but it at first possesses them abundantly in the middle layer of the proglottides, where they afterwards often almost wholly vanish in the more mature stages. We are irresistibly reminded of the history of the so-called "crab-stones," which are known to represent reserve materials; and we are well aware of various epochs in the life-history of Cestodes when there is a temporary demand for a large quantity of lime, and especially of carbonate of lime,—*e.g.*, to neutralise the acid digestive juices, and to form and harden the egg-shells.

Phosphoric, carbonic, hydrochloric, and sulphuric acids have also been detected. The ashes yielded a smaller quantity—only 4·9 per cent.—but this was in the case of a specimen of *Tænia solium* which had been kept for long in spirits.

Virchow first suggested that the calcareous bodies of the Cestodes arose from connective-tissue corpuscles; but although the majority of subsequent observers have supported this opinion—and Schiefferdecker considers that he has even followed the process through all its phases,[1] —the cellular origin of these bodies seems now hardly plausible after Harting's[2] beautiful investigations, in which he shows the origin of the various forms occurring so abundantly among the lower animals, and particularly of those which now interest us. The presence of a formed specific organic substratum is by no means necessary, as was formerly believed; it is sufficient if an amorphous or fluid organic substance be present, with which the carbonate of lime may incorporate itself. If the formation occur in ordinary albumen, then calcareous bodies arise of exactly the same form and nature as those of the Cestodes, agreeing with them also in that they exhibit the same clear residue ("Caleoglobulin," Harting) after dissolving away the lime, and they repeat in their individual divergenees all the variations above noted.

There remains, indeed, no reason for connecting the origin of these calcareous bodies with any special cellular structures in the body of the Cestodes. From suitable preparations, and especially from the larval cystic stage at the time of the formation of the head, one can distinctly convince oneself that they arise without the help of cells. They originate as small roundish grains, having from the first their peculiar optical and chemical properties, and attain their subsequent size by peripheral growth, *i.e.*, by the deposition of successive sheaths.

All the intermediate stages observed between the calcareous bodies and connective tissue cells are, in my opinion, merely concretions, with slightly or unequally distributed lime contents—that is to say, calcareous bodies which contain only a small quantity of inorganic substance, either because it has only been partially deposited, or because the degeneration above referred to has set in.

The Cuticle.—On its surface the parenchyma of the Cestodes bears a clear unciliated elastic skin, which shows no trace of its elementary

[1] Schiefferdecker describes the development of the calcareous bodies as follows (*loc. cit.*, p. 470):—"The doubtful cell first surrounds itself with a membrane. The protoplasm has not its normal appearance; the granules are further separated; it looks as though the cell-contents were diluted. The cell becomes more and more invaded by fluid, the protoplasm shrinks round about the nucleus, which then looks like a ball floating in the fluid contents of the cell. The protoplasm seems still further to disappear,—at least only the nucleus remains, and that without its nucleolus. The calcification begins from the nucleus, it works its way out in distinct zones to the periphery, till the calcareous body is finished. I have never seen any connection between the calcareous bodies and the excretory canals, nor can I tell why so many connective tissue cells calcify."

[2] "Recherches de morphologie synthétique, &c.," *Naturk. Verh. koninkl. Akad.*, Deel xiii.: Amsterdam, 1873.

composition, but is perfectly homogeneous. Both in this respect and in its chemical composition (as shown with regard to *Echinococcus*) this skin reveals its essentially cuticular nature. The thickness of this cuticle varies exceedingly, and not always in proportion to the size of the animal, although as a rule the larger species have the thicker covering. It ought not, of course, to be overlooked that the thickness and firmness of the cuticle is very different at different parts of the body. The cuticle is thickest in the bladder-worm of *Tænia echinococcus*, which sometimes grows to the size of a child's head, or even larger. In this case it shows a very striking lamination, often hardly perceptible in other cases. When the cuticle attains a certain thickness, it possesses a more or less distinct vertical striation, which is, of course, fine, and only visible by the use of a high power. This is of great importance, however, for these organisms, since it is caused by the presence of thickset pores, by means of which the absorptive power of the skin—the only absorbing organ in these asplanchnic Cestodes—is greatly increased. The pores can sometimes be observed on surface inspection as fine, thickly studded little points, some bright, some dark, according to position of the microscope-tube.

We owe the detection of these pores to the researches of Sommer and Landois, whose results have been fully confirmed by subsequent observers. All unite, too, in emphasising their nutritive importance, but this is represented in a way which I cannot but consider erroneous. According to this theory, the pores are not in themselves directly efficient in nutrition, but only in so far as they serve for the protrusion of fine protoplasmie threads, which are in direct continuity with the subcuticular tissue to which they thus pass on the food. This theory is especially maintained by Schiefferdecker, who has tried to establish it to the minutest details.

In suitable preparations it is not difficult to observe, as I have myself done in my earlier investigations, that the cutiele, when intact and of considerable thickness, bears, at certain intervals, a fringe of fine rods or threads. These are about as long as the cuticle is thick, have a granular nature, and "forcibly remind one of similar structures sometimes exhibited on the outer surface of intestinal epithelial eells in Mammalia."[1] They are not unfrequently "so thick that they look as though the outer surface of the worm were covered with a thin layer of granular protoplasm."[1] I attached no special physiological importance to these structures, simply because I eould only regard them as anatomically very unimportant, namely, as the remains of an older exfoliated and altered cuticle, or, in other words,

[1] Quoted from Landois and Sommer (*loc. cit.*).

as the result of a moulting. This opinion I still maintain, even more firmly than ever, and believe that I can support it on indisputable grounds.

I base my arguments mainly upon the state of affairs in the bladder-worms, where this outer fringe may be quite regularly observed, but not on the absorptive, *i.e.*, the outer surface of the bladder, but in a situation where this is impossible—namely, in the canal-like interior space of the so-called head, which is merely the future head of the tape-worm in its invaginated state.

The cuticle which clothes this head is therefore turned inwards towards the above-mentioned canal space, and is repeatedly thrown off and changed as the head rapidly grows. The cast cuticles remain lying in the interior of the space, and more or less fill it. They have exactly the finely granular appearance and the loose texture of the usual fringe, except that they usually hang together as a membrane, and only rarely, and that imperfectly, fall into rods. The outer—that is, the youngest of these layers—for two or three can sometimes be distinguished—is in more or less close connection with the cuticle, just as is the fringe with the cuticle of the tape-worm.

I attach no special weight to the fact that the latter often takes the form of a border of more or less distinct rods. This certainly does not occur so generally and constantly as we are led to infer from the reports of Schiefferdecker and Steudener, who speak of nothing but "little hairs," or "cilia." It is, indeed, occasioned by the rupture which follows in consequence of the increase of surface in the growing proglottides, by forces, therefore, which were not so powerful in the inverted head of the bladder-worm, which was restricted in its longitudinal extension. I need hardly notice further that the presence of the pore-canals must be a factor in the process. The liberation of the so-called "covering membrane" on the above-mentioned epithelial cells is only possible because of the pore-canals which penetrate it.[1]

When I finally note that the connection between the protoplasmic threads and the subcuticular tissue has never been seen by any one, but only imagined for the sake of the theory, and seems in the highest degree improbable when we consider the histological structure of this tissue, then I think I have said enough to show how untenable that theory is, which attempts fundamentally to alter our conception of the nature of endosmotic nutrition.

The cuticle is, on the whole, flat and smooth, but is raised at certain points into little hairs, prickles, and hooks, which vary extremely in form and size.

[1] Compare also similar conditions in the cuticle of the tubules of Rainey or Miescher (p. 201).

The most conspicuous and important of these elevations are the hooks which are situated on the apex of the Cestode head, and which are instrumental in fixing the head, and hence the whole worm, to the intestinal wall of the host. The structure and arrangement of these hooks are also of great systematic importance, as we shall see in the course of our exposition.

The study of the development of these organs shows that not only are all the hooks reducible to the same primitive form, but also that hooks, spines, and little bristles, in fact all the cuticular appendages, are referable to a common type. This primitive form is simply a little cone, seated on a papilliform elevation of the subcuticula, and arising from the hardening of its outer surface, which is at other points also sometimes of a firmer character. If these

Fig. 146.—Development of the hooks of *Tænia serrata*.

cones remain small and thin-walled, then we have the common form of hair or spine. When they grow gradually stronger and bend, and when the continued deposition of skeletal substance renders them even harder, then there arise the characteristic forms of the true hooks. Finally and particularly, in the *Tæniæ* they develop a special process on their lower border, and having formed a well-developed basis or root, become the familiar independent and often even moveable hooks.

The fully developed hook has a very considerable strength, owing to the thickness of its walls, and to the deposition of carbonate of lime. This strength is gradually acquired as the layers are deposited internally, and slowly hardened. In many cases one can detect the successive layers, even in the full-grown hooks, by the lines running down the hook parallel to the outer surface. The thicker the wall the narrower does the internal space become, and in many species it wholly vanishes.

The Subcuticular Layer.—We usually regard the cuticle of animals as the excretion of an epithelial layer of cells, and we often find, lying below it, a tissue of more or less distinct cellular character. Such a subcuticular layer has often been sought for in the Cestodes. I

was formerly of opinion that the analogue of the ordinary subcuticula was to be found in a "richly granular parenchymatous layer," discovered by me under the cuticle. Although this layer has a peculiar structure, and is but imperfectly marked off from the subjacent tissue, my opinion was followed by subsequent observers, except Rindfleisch,[1] and the layer in question was even credited with a distinct cellular structure. The most distinct description is furnished by Steudener, who asserts that the subcuticular layer consists, in all Cestodes, of extended, narrow, conical cells, which stand together like a palisade, with the summits of the cones directed inwards, and with the bases resting on the cuticle. Each cell has an oval nucleus, often slightly broader than the cell itself, which, therefore, must bulge out at that point. The nuclei lie in the middle of the cell, sometimes nearer the summit, sometimes nearer the base, so that in a vertical section they are not seen in a line, but irregularly alternating in a somewhat broad zone. The two halves of these cells differ strikingly in their optical and histological characters, for the basal portions are homogeneous, while the other halves consist, according to Steudener, of a granular protoplasm, in which the boundaries of the cells are but faintly distinguishable.

An inspection of sufficiently thin and well-stained preparations of *Tænia* is quite enough definitely to prove that this sub-cuticular layer is formed, not of mere granules, but of cells usually arranged perpendicularly to the cuticle. It is not, however, so easy to accept Steudener's reports as to the nature of these cells. I am unable to resolve the finely granular outer layer into tops of individual cells, and cannot therefore regard them as cylindrical cells. They seem to me rather, as they formerly appeared to Rindfleisch and Schiefferdecker, as spindle-shaped cells, whose protoplasm lies round about the oval nucleus in a thin layer, and runs out at both ends into thin threads. The outer ends lie against the cuticle, while the inner threads may be followed some distance into the body-parenchyma, and, as I have often observed, may come into distinct connection with the very fine transverse muscular fibres.

Nor can I recognise in these cells the matrix cells of the cuticle, but agree with Rindfleisch in regarding them merely as peculiarly formed connective tissue cells. I am further confirmed in this opinion, since the cells in question sometimes lose their spindle form, and look exactly like the connective tissue cells of the Cestodes. Thus it is, for example, in the head of the tape-worms, in the parts connecting the individual joints of *Tænia saginata* (Fig. 147), and in the leaf-like

[1] "Zur Histologie der Cestoden," *Archiv f. mikrosk. Anat.*, Bd. i., p. 140, 1865.

or lappet-like prolongations of the side-walls of *T. perfoliata*. Hence the transverse muscles are but slightly developed at these points, and I feel almost inclined to suppose that there is some connection between them and the spindle-shaped cells, especially since the latter have, as has been mentioned, been seen in direct connection with the former. When one further notes that the direction of the spindle-cells in the long-jointed *Tæniæ* (*Tænia saginata*, &c.) varies at the ends of the proglottides in conformity with the muscle-fibres, one feels almost warranted in regarding the spindle-shaped or subcuticular cells as a sort of tendinous fibres.

In agreement with this we may note that the spindle form of the cells in question is but inconspicuous in the *Bothriocephali* (*B. latus*), which have a poorly developed musculature. The filiform ends are extremely delicate, and are very easily overlooked; the cells themselves are closely grouped together in a thick layer. With the exception of the peculiar grouping, they exactly resemble the ordinary connective-tissue cells of the rest of the parenchyma.

If the above theory of the subcuticula be correct, then the Cestodes have no epithelial membrane covering the body, and the same will be true of the Trematodes. The cuticle cannot be genetically compared with the cuticle of the lower animals; it is rather the structureless limiting membrane of the connective-tissue substance, and is comparable with the so-called basement membrane found in the other flat-worms, and especially in the Planarians, between the muscular layer and the dermal epithelium.

This is, indeed, a theory which has been formerly repeatedly maintained, particularly by Schneider,[1] and was suggested especially in connection with the embryos of some species which throw off their ciliated epithelium. Minot reports having seen, even in the adult stages of *Caryophyllæus*, *Tænia*, *Bothriocephalus*, &c., distinct cylindrical cells on the uninjured cuticle.[2] This must, however, rest on a confusion with the above described excreted layer.

The histological and chemical nature of the Cestode cuticle can hardly be used as an argument against regarding it as comparable to the basilar membrane, for we know that in the lower animals the connective substance occasionally assumes a thoroughly cuticular character.[3] The only argument against this theory is the dogma according to which the outer surface of every animal should during

[1] "Untersuchungen über Plathelminthen," *Vierzehnter Bericht d. oberhess. Gesellsch. Natur- u. Heilkunde*, p. 69, 1873.

[2] "Studien an Turbellarien" (*loc. cit.*), p. 456.

[3] I may refer to my observations on the intermuscular connective substance of the Nematoda and Acanthocephali: see Vol. II.

life be clad with an epithelial layer—the ectoderm. But general statements of this kind must vary with the growth of our experience, and it is only to the results of experience that we can attach decisive importance.

Yet another argument against the prevalent explanation of the so-called subcuticula as an epithelial layer is found in the fact that it is not directly adjacent to the cuticle, but is in fact separated from it by a layer of fibres crossing at right angles.

Our attention is first directed to the existence of this peripheral fibrous layer by the appearance of a thin section of the skin, which shows on its surface a delicate, extremely fine lattice-work. The lines, which form this, run very regularly transversely and longitudinally, and turn out on further examination to be the contours of fibres, which are arranged one over the other in simple layers. The outermost are the transverse or circular fibres, which form a continuous sheath, while the longitudinal fibres are separated by interspaces, through which run the external processes of the spindle-shaped cells.

This difference between the two layers of fibres is obviously the reason why many investigators have claimed for each a distinctive character. The longitudinal fibres have been very generally regarded as muscles, but those running circularly have sometimes been regarded as connective-tissue fibrils (Rindfleisch), and sometimes as integral parts of the cuticle (Schiefferdecker and Steudener). Only a few observers (Leuckart, Nitsche, Schneider) have regarded them as a layer of circular muscle fibres.

I still hold to the last opinion, because if the fibres of the two layers be observed under the same conditions, they have the same optical characters; and, besides, there are cases, as in the so-called caudal bladder of the *Cysticerci,* where both circular and longitudinal fibres are in their thickness and microscopic characters undeniably muscular. They are indeed usually paler and narrower than most muscle fibres, but these present so many striking differences that one cannot lay much weight on such peculiarities.

After this discussion of the facts of the case, I do not think that I am wrong in claiming the subcuticular fibrous structure of the Cestodes as a musculo-dermal layer.[1] The other muscles penetrating the connective substance of the body might then be called the parenchymal muscular system.

[1] Previous investigators have also sometimes spoken of a musculo-dermal layer in the Cestodes, meaning thereby usually the muscles of the cortical sheath, including generally the transverse fibres surrounding the middle layer. These I designated, not quite correctly, in the first edition of this work as the layer of circular fibres, and indeed as the "deeper" or "inner" layer, as distinguished from the subcuticular system.

The Muscular System.—The fibres of which this consists are sometimes separate, sometimes united, but in the adult stages run so regularly in the three dimensions of space, that one can fitly designate them longitudinal, transverse, and sagittal muscles. As in other animals without a skeleton adapted for locomotion, these muscles are wholly composed of smooth or so-called "organic" fibres. One looks indeed in vain for a nucleus, at least in those which are full-grown. They consist of a perfectly homogeneous, strongly refractive protoplasm, showing at most, and that only in the thick fibres, a differentiation into peripheral and axial substance. The ends are narrowed and drawn out into more or less long threads, not unfrequently dichotomising. On the isolated fibres one often sees lateral processes, as thin, delicate filaments, forming sometimes a distinct network. One may even hazard the supposition that the intercellular network above described was of a muscular nature.

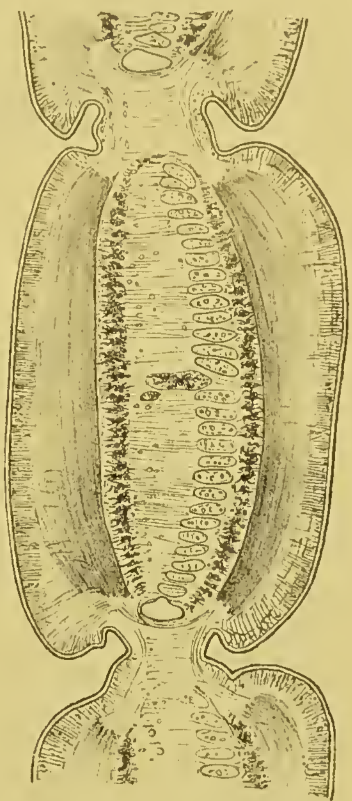


Fig. 147.—Longitudinal section of *Tænia saginata* (young chain of joints). (× 25.)

These parenchymal muscles attain their greatest development in the musculi longitudinales which occur in all Cestodes, and which run, especially down the inner part of the cortical layer, in the form of numerous strong bands (Fig. 147). This is most distinctly and most beautifully seen in the younger joints, where the fibres are arranged in closer groups, though they are of course much shorter than is afterwards the case. These deeper bands exhibit the thickest fibres—the thickest, indeed, in the whole body. Externally both bundles and fibres thin off, sometimes gradually, sometimes suddenly, until in the close neighbourhood of the cuticle we only find the fine isolated fibres. In many cases these can be followed into the longitudinal fibres of the musculo-dermal sheath, so that the distinction between the two systems becomes somewhat fictitious.

Like the longitudinal muscles, those which run transversely are usually well developed, and grouped in bands of considerable strength. This is at least true of the main mass of those fibres, which bound the middle layer, and which (except in *Tænia undulata* and a few others) are almost united into a continuous layer, lying

under the longitudinal bands. With a low power it often appears as though we could, in a cross section, follow these fibres in a ring round the middle layer (Fig. 144), but in reality we have here to do with two flat muscular plates, whose fibrous bands enclose the middle layer, and expand at the sides of the joints (Fig. 148) into

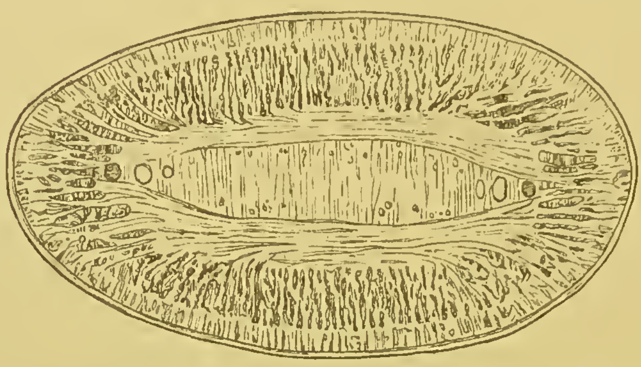


FIG. 148.—Cross section of a somewhat older joint of *Tænia saginata.* (× 38.)

a fan shape towards the cuticle. Inasmuch as the bundles on either side often converge, and even occasionally cross, it appears as if they were in continuous connection; and this is especially so, since many of the sagittal muscles also usually bend round, and surround the middle layer. It is not, however, only at the lateral borders of the joint that the transverse fibres bend from their normal direction towards the cuticle; the same appearance is to be observed (Fig. 148) here and there throughout the rest of their course. This occurs sometimes at so many points, especially in the young joints, that the longitudinal muscles, separated by the processes, assume an almost radiate arrangement, and present an appearance which reminds one of the fibrous groups in the cortical layer of the spinal cord.

Finally, as to the sagittal muscular fibres, these are mostly isolated or united in slender bundles, which are stretched between the two surfaces of the tape-worm, and were hence originally described by me as dorso-ventral muscles. They are the thinnest of all the parenchymal fibres, and run as fine fibrils almost straight across the whole thickness of the body through both layers. In the outer layer they form almost the only contractile elements, other muscle fibres being but rarely present to any considerable extent. It is, however, only in their earlier stages that the sagittal fibres run at all straight, for the development of the generative organs which finally grow throughout the whole of the middle layer naturally influences their arrangement, and often alters their direction.

It is not necessary to enter into details as to the working of the above-described muscles. It is easy to understand that the longitudinal fibres shorten the body, while the other muscles give rise to elongation by lessening the diameter. Their action is aided by their general connection with the cuticle, as well as with the surrounding body-parenchyma. We have already emphasised this fact, and also the probable function of the subcuticular cells.

It is not only the transverse and sagittal fibres which exhibit a connection with the latter. It can also be demonstrated of the longitudinal fibres, at least in those cases where the individual joints are sooner or later separated from one another. Then one sees that the longitudinal fibres do not run continuously throughout the whole worm, as in the unsegmented forms and in the anterior imperfectly separated portions of other forms, but pass at the joints into a number of fine threads, by means of which they are inserted into the folds of the constricted cuticle.

I am most intimately acquainted with the state of matters in *Tænia saginata,* in which there is an almost neck-like isthmus connecting two adjacent joints, in itself well marked off from the rest of the body-mass, both histologically and otherwise. Especially one is struck with the poverty of the musculature, and with the absence of the spindle-shaped cells, usually placed at right angles to the cuticle. Muscles are not, however, wholly absent. With a high power one can recognise a number, not only of sagittal but also transverse fibres; both are, however, much sparser, and, the latter especially, markedly thinner than usual. No longitudinal fibres can be detected. They all end near the boundary of the joint, sharply and suddenly, so that there is no doubt that the joints are, thus far at least, independent. The connection between them is effected by spindle cells, which look exactly like those of the subcuticula, except that they are not seated on the cuticle, but are embedded longitudinally in the clear ground mass. Here and there one can plainly see how the fine end of a fibre comes into union with a connective-tissue fibril, and is thence connected by a whole

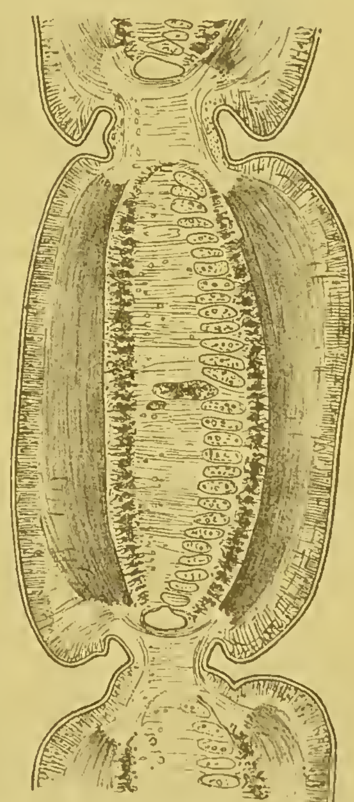


Fig. 149. — Longitudinal section of *Tænia saginata.* (× 25.)

series of spindle cells with the longitudinal musculature of the neighbouring joint. It is, however, only the deeper layer of the longitudinal muscles which exhibits this relation. The more superficial fibres have indeed their spindle cells, but these bend at an early stage out of their longitudinal direction and attach themselves to the cuticle. They resemble the ordinary subcuticular cells, except in this, that they do not lie at right angles to the cuticle, but at an acute angle corresponding to the direction of the connected fibres. This cannot, of course, be considered an essential difference, since even the subcuticular spindle-cells bend from their normal direction at the incurved terminal borders of the proglottides, and apply themselves to the cross muscular fibres, here bent into the form of a bow (Fig. 149).

These arrangements are best studied on sagittal longitudinal sections, which show us further that (Fig. 149) the middle layer of the individual proglottides, although passing through the isthmuses without interruption, and thus, like the cortical layer, running the whole length of the worm without breach of continuity, differs widely at various situations in the structure of its sagittal muscles. Not only do these become considerably stronger at the ends, but they curve into little arches, as has been already noted (p. 291). In this way the generative organs are, to some extent, bounded and restricted in the individual joints.

Fig. 150.—Four last joints of *Tænia saginata* about to be liberated. Nat. size.

There is no need to point out how much the liberation of the proglottides is facilitated by the above arrangements. It is also evident that the liberation will be effected by muscular contraction. I believe that the sagittal muscles are by their structure specially efficacious in the process of liberation, for they are able by contraction to flatten themselves, and thus considerably to expand the middle layer. It is, indeed, the middle layer which first ruptures, while the peripheral parts, and especially the lateral borders, often retain their connection for a while (Fig. 150).

In the interior of the head the arrangement of the muscles has been specially modified on account of the presence of suckers and hooks. The various muscle-groups of the body can be followed a considerable distance through the "neck," but their arrangement varies very much according to the nature of the attaching apparatus. We will now simply refer to the detailed description which we shall afterwards give of the head both in *Tænia* and in *Bothriocephalus*, and will only note that these two types do not by any means exhaust the existing modifications.

The musculature of the head is not always limited to the hitherto discussed groups of fibres. Special, more or less complex, muscular arrangements are brought into requisition for moving the suckers, and also sometimes the hooks, as in *Tænia*. The most peculiar modifications are found in *Tænia* (Fig. 151) and *Tetrarhynchus,* in which not only have the suckers a specially strong and complex musculature, but the hooks are seated on a more or less proboscis-like muscular apparatus (four of which are present in *Tetrarhynchus*), which finds a parallel only in the Acanthocephali.

Similarly, there are usually special muscles in connection with the penis, to which we shall afterwards return.

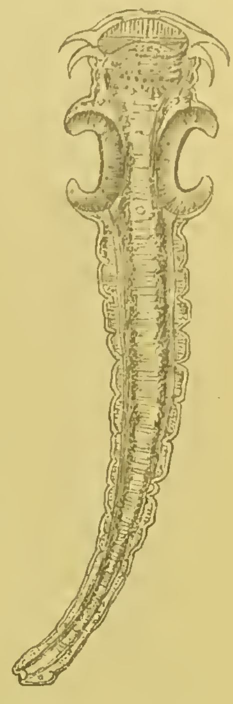


FIG. 151.—Longitudinal section of a young *Tænia serrata,* consisting mainly of head and neck. (× 60.)

The Nervous System.—When we consider the development of the muscles, it seems strange that the nervous system has long been sought for in vain. It is true that some investigators have described a central ganglion in the head of certain species, and especially in *Tetrarhynchus,* which is distinguished by the large size of that part of the body. I recall especially the observations of J. Müller and Wagener, but they have still left us without any real proof of the correctness of their representations. Thus, the existence of a nervous system in the Cestodes long remained a moot-point, and that the more naturally since the reports as to the nature of the ganglionic apparatus contradicted one another, and the great majority of observers had to declare themselves unable to find anything which could be with certainty denoted as a nervous system.

And yet the Cestodes do possess a nervous system, and a well developed one, with a central part lying inside the head, and with two distinct lateral cords which run continuously down the whole chain of joints, and which sometimes, as in the larger species of *Tænia* and *Tetrarhynchus,* break up into several strands running side by side. In *Tænia* they lie outside the excretory canals, and are easily detected in transverse sections. That they have hitherto been generally overlooked is largely due to the fact that they are destitute of any independent sheath, and consist of but slightly specialised tissue. They have not, of course, remained wholly unobserved. For not only was the cephalic ganglion described by the older observers in *Tetrarhynchus,* partly at least, as really related to the nervous system,[1]

[1] See especially Wagener's representation, "Entwickelung der Cestoden," *Den naturk. Verhandl. holländ. Maatschappy:* Haarlem, pl. iv., 1857.

but the same must be said of the "plasmatic longitudinal vessels," described by Sommer and Landois, and referred by them to the alimentary system.[1] Similarly Bötticher described the cephalic ganglion of *Bothriocephalus latus* as an anastomosis of excretory vessels,[2] and I have myself regarded the lateral nerves of *B. cordatus* as of a vascular nature.[3]

Schneider was the first to identify these structures as nerves, and observed a wide anastomosis formed by them in the head of *Ligula* and *Tænia perfoliata.* His identification was not based so much on their histological structure as upon their anatomical resemblance to the nervous system of Nemertines. The resemblance includes among other points this, that in both *Tænia perfoliata* and the Nemertines the nerve cords are lined with eells towards their ventral and dorsal surfaces. Schiefferdecker has supported Schneider's conclusion, trusting mainly to the results of a histological investigation, according to which the so-called "vessels" are resolved into spongy tracts, consisting of fibrils with layers of very delicate fragile cells. Schiefferdecker believes further that he has found peripheral nerve endings, both on the muscular fibres, where they have the form of the so-called "terminal triangles," and also as independent structures, something like Pacinian bodies (0·011–0·017 mm. long by 0·004–0·006 mm. broad) distributed through the body-parenchyma of *T. solium*, *T. elliptica*, and especially abundant between the thick fibrous bundles of the musculi transversales.

The almost contemporaneous researches of Blumberg[4] and Steudener, and the essentially corroboratory results of my pupil Kahane, with which my own observations lead me to concur, may be held as decisive as to the presence and general nature of the nervous system.[5]

FIG. 152.—Nervous system of *Tænia perfoliata.* (× 20.)

The cephalic ganglionic mass consists of a tolerably thick transverse band, which in *Tænia* lies somewhat deep below the proboscis or so-called "rostellum," but which in *Bothriocephalus* and *Tetrarhynchus* is somewhat approximated to the upper surface of the head. The ends of

[1] In *Tænia* these strands were erroneously described as simple canals, and as lying in the inside of the excretory vessels; *Zeitschr. f. wiss. Zool.*, Bd. xxiv., p. 515, note, 1874; see Nitsche, *ibid.*, Bd. xxiii., p. 191, 1873.

[2] *Archiv f. pathol. Anat.*, Bd. xxx., p. 109, 1864.

[3] First German edition of this work, Bd. i., p. 445.

[4] "Ein Beitrag zur Anatomie der Tænia plicata, T. perfoliata und T. mamillana," *Archiv f. wiss. u. pract. Thierheilk.*, Bd. i., p. 23, 1877.

[5] [See also the later investigations of Pintner, "Untersuchungen über den Bau des Bandwurmkörpers," pp. 67, *et seq.*: Wien, 1880.—R. L.]

this nervous mass, corresponding to the sides of the head, are usually thicker than the band stretching between them, though we are not warranted by the histology in regarding them as two ganglia united by a commissure, as Blumberg[1] and others have done. A strong nerve cord runs backwards from each of these lateral swellings, and since they are almost as broad as the latter, they look like direct prolongations. Each passes outwards in a curved course, and, entering the body, becomes one of the above-mentioned lateral nerves which run down the middle layer close by the border,[2] to which they sometimes send an external branch. Such is the case in *Tænia perfoliata*, where also one can observe, opposite the origin of the lateral nerves, another branch, which runs forward between the suckers, evidently designed to supply the head.

It is difficult to analyse the histological structure of these nerves, and the accounts of their nature vary widely. In *Tænia perfoliata* I can recognise, like Kahane, a distinctly fibrous texture in the finely granular clear mass of the cephalic ganglion, and also lying between the fibres, numerous small (0·015–0·025 mm.) ganglion cells with a nucleus, and membraneless, granular protoplasm. These are to be found both in the median commissure and in the lateral swellings, and have usually an oval or triangular form, which is probably to be regarded as related to the presence of fibrous processes, especially since the long diameter of the cell is always in a line with the direction of the fibres. Although these cells are by no means sparsely distributed through the ganglion mass, I cannot at all agree with Blumberg in regarding the latter as merely a conglomerate of ganglion cells. In Steudener's preparations the cells had fallen into pieces, and their presence was only indicated by the "somewhat large round nuclei with nucleoli" which remained.

The histological analysis is rendered more difficult by the fact that the nerve substance is penetrated throughout by a fine meshwork of supporting tissue, which is not striking in *Tænia perfoliata*, but is in some other cases strongly developed (in *Tænia crassicollis*, according to Steudener). This meshwork is also found in the lateral nerves, where it sometimes predominates so much over the fibres that the early observers spoke of it as "spongy cords." Here and there Kahane and I have both been able to detect distinct cellular structures; but, on the other hand, I have never been able to discover the

[1] Blumberg shows (*loc. cit.* Tab. i., Fig. 1), besides the two main masses, also a third in the sagittal space between the suckers, and speaks in the text of several aggregations of ganglion cells connected by nerve filaments.

[2] We have already noted how Sommer erroneously places the lateral nervous cords of *Tænia saginata* inside the longitudinal vessels ; *Zeitschr. f. wiss. Zool.*, Bd. xxiv., Tab. xliii. and xliv., 1874.

layer of cells which Schneider described as lying on the dorsal and ventral surface.

The Alimentary System.—We have already noted how the structure of the Cestodes is simplified by the absence of these organs. Nor is it the alimentary canal alone which is wanting, but blood-vessels and blood are also sought for in vain. The transference of the nutritive fluid is wholly effected by osmosis as in the other bloodless animals, which include a great many of the parenchymatous worms.

Attempts have, indeed, been made to credit the Cestodes with these structures. It used to be very common to describe an alimentary canal, and even a two-lobed one, as in the majority of the Trematodes. Observers spoke of two vascular canals running laterally throughout the whole chain, and opening to the exterior, sometimes on the top of the head, sometimes by the suckers. Longitudinal canals the Cestodes certainly do possess, which run uninterruptedly from head to terminal joint, and which are sometimes straight, or sometimes bent into zigzag folds, according to the state of contraction exhibited by the animal. But these canals are not alimentary; they have no mouth opening to the exterior; they contain no chyme, but only a clear watery fluid, without granules, and at most yielding a finely granular precipitate on treatment with certain reagents (absolute alcohol). This substance is occasionally expelled in the form of little pillars of varying length. The chemical analysis of these masses yields, according to Sommer, substances which are related to xanthin and guanin.

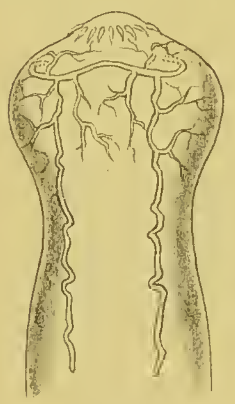


FIG. 153.—Head of *Tænia serrata*, with its excretory vessels (× 24).

The Excretory System.—From what has just been said, we may take it as proven that the longitudinal canals of the Cestodes have an excretory function, as has indeed been for long very generally assumed from the analogy of the Trematodes.[1]

The arrangement of the vessels is not the same in all the Cestodes, nor are they typically two, but rather four in number, particularly in forms with four suckers. Four are generally to be seen in the head, corresponding in position to the suckers, and uniting under the rostellum, when there is one, by means of a simple or plexiform circular vessel.

[1] The term "water vessels," introduced by v. Siebold to denote these canals, is by no means happy. In the first place, the contents do not consist of water, and further, the name is associated with v. Siebold's erroneous idea that the "water vessels" were respiratory ("Vergl. Anat.," pp. 43 and 137, 1848). Further, the term has been used to denote the most diverse structures. See my remarks in Bergmann and Leuckart, "Vergl. Anat. u. Physiol.," p. 284, 1851.

From the head the four vessels pass to the neck of the tape-worm, where, with the increasing breadth, they diverge ever further from one another, till they finally acquire a lateral position.

In many species these lateral stems can be followed throughout the whole chain as four strands, sometimes equally developed, or sometimes with one canal on either side abortive. This unequal growth is seen in very various degrees, and is sometimes much marked, especially in the larger *Tæniæ*, where one canal much narrower has been observed running for some distance considerably to the inside of the larger (see Fig. 148), but gradually disappearing in the broader and thicker joints.[1] Instead of the four canals, there is thus but one on either side, but this has a considerable diameter, which has grown in proportion to the joints. This is the state of the case, *e.g.*, in *Tænia saginata* and *T. solium*, while *T. elliptica* and *T. perfoliata*, on the other hand, are instances of forms where there are two vessels on either side, in the first case unequally, and in the latter almost equally developed.

One must not suppose that these vessels run isolated through the body of the tape-worm. As in the head, so in the joints, they are connected by a transverse anastomosis, by a circular vessel, when four canals are present,[2] or by a simple vessel, where there are only two. The anastomosis always takes place at the posterior border of the joint (Fig. 147), and has about the same diameter as the connected vessels.

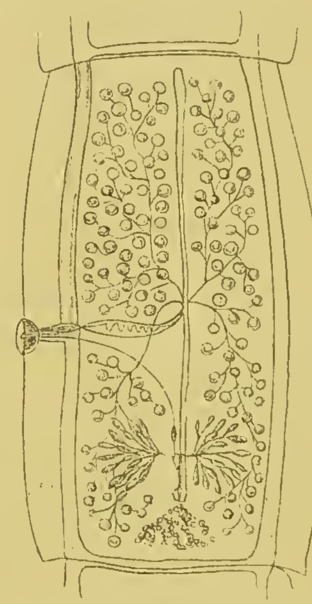


FIG. 154.—Joint of *Tænia cœnurus*, with excretory vessels and generative organs. (× 10.)

We may further note that the width of the vessels is not always equal, but undergoes many changes, which take place indeed only slowly and gradually, but sometimes are so marked as to result in the disappearance of individual vessels. One is sometimes inclined to suppose with v. Siebold (in the case of *Tænia echinococcus*), that the walls of the vessels possess a slight but real

[1] Moniez connects the abortion of these canals, perhaps not without reason, with the formation and growth of the genitalia (*Bull. sci. dep. Nord*, p. 225, 1878). He is, however, wrong in regarding the strands of Sommer, which we have seen to be nerves, as the remains of the aborted vessels. Indeed, he has afterwards recognised their nervous nature (*ibid.*, p. 73, 1879). [According to Pintner's observations, the abortive vessels always lie on the dorsal aspect of the body.—R. L.]

[2] Steudener denies the existence of these circular vessels, and asserts that the communication between the two sides is always effected by a simple cross vessel. This is a mistake, as is proved by Kahane's researches on *Tænia perfoliata*.

power of contracting, were it not, however, possible that the phenomena observed were due to external pressure or to internal obstruction. At any rate, the vessels—even the widest of them—are without circular muscles. Their walls consist of a clear, structureless cuticular membrane, which is of varying thickness, according to the width of the lumen, but is otherwise without peculiarity. A coating of cells has never been observed, even on the outer surface of the vessels, which is on all sides in direct contact with the connective-tissue substance in which they are embedded.

Here and there one can observe individual fibres attaching themselves to the walls of the vessels. The connection is effected by means of a small wing-like or conical terminal piece, which is somewhat like the so-called "terminal triangle" of the motor nerve fibres. I can hardly doubt that these fibres have a muscular character, and that they are able to affect the width of the vessels, especially since they lie at right angles to the walls. If we suppose, what is indeed warranted by the optical characters of the walls, that the canal system of the Cestodes is in a state of elastic tension, even when the vessels are moderately full, then the presence of these special dilators is very natural, and well suited to increase or to oppose the action of obstruction or pressure, as the case may be. The local limitation of these actions is readily intelligible, since the contents of the vessels can only move backwards, in spite of the continuity of the whole system. It has never been found possible to fill the longitudinal stems by injecting substances from behind forwards, while there is no difficulty in driving the fluid from the head downwards through a long stretch of joints. This is explained by the presence of a valvular arrangement, which is formed (according to Platner and Sommer) by two opposite folds or duplicatures of the walls, which project into the lumen at a point above the transverse anastomoses.

This arrangement would of course result in a constant accumulation of excreted matter in the posterior joints, were there not some means for its removal. And so there is, for at the end of the last joint the vascular apparatus opens to the exterior.

This is generally effected by means of the transverse anastomoses. In the posterior joints which are sharply divided from one another, the transverse branches shorten according to the depth of the constriction, and finally, when the joints separate and the vessels rupture, the line of anastomosis becomes a cross cleft. This has no great length, and, curving forward, assumes a sort of bladder-like form, while the line of rupture is at the same time drawn together. It is this bladder which receives the longitudinal vessels and conducts their contents to the exterior, for which function it is specially fitted by the presence of the

circular muscles of the body which surround it, and are thus able to cause it to contract.[1]

What I have said above as to the excretory apparatus of the Cestodes is primarily applicable only to those species with four suckers. In *Bothriocephalus*, which has only two suctorial grooves on the surface of the head, the structure of the canals is somewhat different, since the longitudinal canals are not only increased in number, but are very thoroughly connected by numerous transverse and oblique anastomoses, which are quite independent of the joints and form a more or less close meshwork. Usually there are eight of these longitudinal vessels, which are equally distributed on either side, but there are cases where sixteen and even more appear, though not all necessarily of the same size. Towards the head, these canals usually run together till only two main stems are left. It is doubtful whether these are united in a loop, as in *Tænia*, but in some species at least this is not so. At the posterior end one finds a distinct opening in the form of a bowl or bladder-like depression into which the longitudinal canals run. This structure is most conspicuous and independent in *Caryophyllæus*, which, as is well known, has no joints, and in which, therefore, the posterior extremity is permanent. It has formed a longish tube, which exhibits a distinct pulsation effected by the musculature investing its cuticle.[2]

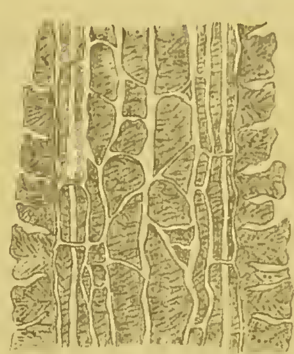


FIG. 155.—Excretory apparatus of *Bothriocephalus proboscideus*, after Steudener. (× 32.)

The above-mentioned network of vessels is not the only structure of the kind to be found in *Bothriocephalus*. In small transparent worms, which can readily be investigated alive, one can convince oneself of the existence of a system of fine, richly ramified and

[1] Wagener describes special excretory openings in the anterior end of many Cestodes ("Entwickelung d. Cestoden," Breslau, 1854: *Nova Acta Cæs.-Leop. Acad.*, Bd. xxiv., Suppl.), which are connected with the longitudinal vessels by short cross branches. Both Kölliker and I think we have occasionally observed these openings. Hoffman has lately described similar openings in *Tetrarhynchus*, not, however, behind the suckers, but before them, and in fewer numbers also on the anterior lateral borders ("Ueber den encystirten Scolex von Tetrarhynchus," *Niederländ. Archiv f. Naturw.*, Bd. v., Heft. i., p. 1, 1879).—[The investigations of Fraipont (*Archiv. d. Biol.*, t. ii, p. 10, 1881) have shown that such secondary openings are by no means uncommon in tape-worms. In *Ligula*, where Riehm (*Corresp.-Bl. d. Naturw. Ver. f. Sachsen u. Thüringen*, p. 276, 1882) observed them, they were arranged in regular metameric fashion. Pintner (*loc. cit.*, p. 31), in contradiction to the above, remarks that the longitudinal vessels always open singly at the hinder margin of the joints.—R. L.]

[2] According to Steudener, this funnel-shaped organ is, even in the case of *Caryophyllæus*, only a depression of the posterior extremity.

interlaced vessels, lying in the more superficial parenchyma, and partly close under the cuticle. Though not uniformly developed, these vessels are distributed over the whole body, and are connected so frequently and distinctly with the larger stems as to leave no doubt as to the relations of the two systems. The finer vessels obviously form the proper excretory apparatus, being suited to act as simple filters by the structureless nature of their walls, whilst the coarser canals are the efferent ducts. Here and there, doubtless, subsidiary functions are discharged; for example, the abundant development of the fine network, in the head especially, in forms with complex suctorial organs, leads one to conjecture that they act as a sort of *corpora cavernosa* in the expansion of the suckers.

As in *Bothriocephalus* so is it in the other tape-worms, even in *Tænia*, as one can observe in fresh clear specimens of say *Tænia elliptica*. It is not, indeed, always possible to follow the capillary system for a long distance without interruption, since the individual vessels often seem to disappear and crop up again at other places. Nor are their relations to the longitudinal canals equally distinct throughout.[1]

What specially attracts the attention of the observer to this peripheral apparatus, is the presence of small, continually waving, cilia-like lappets which are situated on the inner wall of the vessels, especially at the clefts, and which serve to keep up a continuous movement of the fluid, independent of the contractions of the body. In suitable specimens, such as *Tænia elliptica*, and especially in *Triænophorus*, it is not difficult, with a little careful observation and with a high power, to detect these cilia-like lappets,[2] and they have been noticed by v. Siebold, M. Schultze, and others. Their existence has, however, been lately called in question, especially by Steudener. The cause of this mistaken criticism is to be found mainly in the too exclusive examination of sections instead of living animals, and also doubtless in the use of large opaque tape-worms, which, though more readily obtainable for examination, are but little suited for deciding the point in question.

But not only did the cilia-like apparatus escape observation, but even the capillary vessels in which the former are situated. Longitudinal stems and anastomoses were held to represent the whole excre-

[1] It is a striking fact in this connection that the peripheral network cannot be injected by way of the longitudinal vessels. This is perhaps due to the existence of valves similar to those at the entrance of the cross vessels. We cannot, however, immediately conclude that there is no communication between the systems.

[2] The discovery of these structures is due to G. Wagener, who has also earned our approbation by the demonstration of the above-described capillary excretory system; see "Entwickelung d. Cestoden," *loc. cit.*, p. 14.

tory system; no ramifying side branches were to be seen; at most a few accessory branches have been described in the head, and the suckers are indeed provided (Fig. 153) with a special vessel springing from the above-described circular commissure.

It is also true that now and then vessels are given off from the longitudinal canals, and are sometimes hardly less important than those just mentioned. This is the case, for instance, in *Tænia perfoliata*, as was noted even by Kahane. The vessels pass soon after their origin into the cortical layer, where they ramify, and finally assume a capillary character.[1] The "plasmatic vascular system" observed by Sommer and Landois in *Bothriocephalus latus*, traces of which are also found in *Tænia saginata*, obviously belongs to this capillary system. This, however, only refers to those vessels which pass under the so-called "subcuticula," and are really vessels, for in his later work on *Tænia saginata* Sommer has evidently represented the lateral nerves as part of this apparatus. The vessels are described as fine and very thin-walled passages, which ramify peripherally as well as centrally, and ultimately become united with the processes of connective tissue corpuscles. By means of these cells, and by means of some of the pores of the cuticle, they come into communication even with the external layer. An excretory apparatus, consisting of wider canals, was observed by Knoch[2] and Böttcher,[3] in young and transparent living examples of *Bothriocephalus latus*, but its existence has since been denied.

The designation chosen by Sommer and Landois for the vascular system which they have observed, and the description there given, leave not the slightest doubt that they regard the canals in question as an arrangement for nutritive purposes. This idea is thus a repetition, although in improved form, of an opinion, which we have formerly maintained, and still maintain, to be erroneous, although it has meanwhile found a representative in Blumberg.[4] It is true that, according to the latter, it is not the whole of the surface of the body that serves for the reception of nourishment and for its introduction into the vascular system, but only the inner surface of the suckers, whose cuticular pores are in connection with the spreading terminal processes of the longitudinal canals. "The vessels form, especially at the base of

[1] [According to the observations published by Pintner and Fraipont, in the above-mentioned memoirs, the behaviour of this capillary apparatus is very different from that here described. Its tubes never form a network, but, singly or united in pairs, open into the wider canals, and bear each a ciliated funnel at the outer end. The cilia like lappets are never present in the interior of the tubes.—R. L.]

[2] *Mém. Acad. impér. St. Petersbourg*, t. v., No. 5, Pl. ii., p. 38-38, 1862.

[3] *Archiv f. pathol. Anat.*, Bd. xlvii., p. 370, 1869.

[4] *Loc. cit.*, p. 39.

the suckers, a regular network, which unites into larger stems as it leaves the suckers. In the spaces between the suckers the vessels anastomose. Here originate the longitudinal stems of the body. In *Tænia perfoliata* I observed only two stems,[1] one of which ran down each side of the middle layer of the body. The thickness of the walls is considerable. In every joint the longitudinal canals give out branches, which ramify."

And it is not only fluids which find their way through the pores of the suckers, but formed substances, "roundish bodies of the size of blood or chyle corpuscles." These are found in the intestinal mucous membrane of the host, and are probably nothing else than blood and chyle corpuscles. They are very frequently found in the interior of the suckers, which are sometimes quite full of them. Blumberg thinks that he has also found these corpuscles in the vessels of the suckers, and followed them on their way to the interior; but I must confess that I am of Kahane's opinion, who identifies these so-called corpuscles with cross sections of muscles, and regards the contents of the hollow of the suckers merely as epithelial cells and their remains. After all this, I see no reason for renouncing the old opinion as to the vascular apparatus found in the Cestodes; and the less so since this apparatus has been shown by the elder van Beneden to be most thoroughly homologous with that occurring in the Trematodes, where the presence of an intestine shows, more distinctly than in other cases, that it is to be regarded as an excretory apparatus.

The Sexual Organs.—The structures which we have been considering extend throughout the whole body of the tape-worm, although the various parts may exhibit many differences in the nature and perfection of their development. But it is quite otherwise in regard to the last organ which we have to describe; the great distinction being, in a word, that though common to the joints, it is completely absent from the so-called "head" of the tape-worm. It is true that at first the proglottides are without sexual organs. But their asexuality has only a short duration. As soon as a definite size is reached, the sexual development begins just as is the case in many of the lower animals. The separate parts originate in definite succession, they grow, they perform their functions, and ultimately attain so large a size that the other organs of the Cestode body are quite dwarfed. The uterus is developed most of all, and by the accumulation of the hard-shelled ova it assumes a more or less brownish colour, and renders the appearance of the otherwise peculiar mature joints very striking. This is especially true of the larger species,

[1] This is a mistake, for four longitudinal stems can be plainly distinguished.

such as *Tænia solium* and *Bothriocephalus latus*, whose branched (Fig. 156) or rosette-shaped (Fig. 157) uterus was known to observers as early as the beginning of the last century (since Andry), although it was generally erroneously regarded as an ovary until the time of v. Siebold.[1]

Fig. 156.—Two joints of *Tænia solium* with branched uterus. (× 2.)

But though the sexual organs of the tape-worms are thus very striking, their accurate investigation is involved in great difficulty. It was, of course, soon agreed that the proglottides were provided with male as well as female organs, but the structure and the relation of the various parts eluded for a long time further determination. We have, however, gradually obtained a satisfactory insight into these, thanks especially to the researches of v. Siebold, Sommer and Landois,[2] and myself.

What stands in the way of the analysis of the sexual apparatus of the Cestodes is partly the parenchymatous nature and thickness of the tape-worm body, which almost always necessitate a detailed methodical manipulation, and partly also the complex structure and the thick outline of the various parts. Besides this, the form and structure of the latter often vary considerably from those of nearly related species, and are influenced in an unusual way by the external form of the joints, as will be still more discussed in considering the Tæniadæ.[3]

Proceeding to the general consideration of these sexual organs, I may

Fig. 157.—Female sexual organs of *Bothriocephalus latus*, showing the uterus, ovary, shell-gland, and yolk-gland. (× 12.)

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[1] Concerning the historical development of our knowlege of the sexual organs of the Cestodes, compare especially the statements of Sommer, *Zeitschr. f. wiss. Zool.*, Bd. xxiv., p. 299, 1874.

[2] Besides the formerly mentioned treatise on *Bothriocephalus*, Sommer's later work on the structure and development of the sexual organs of *Tænia mediocanellata* and *T. solium* (*Zeitschr. f. wiss. Zool., loc. cit., supra*) deserves special mention.

[3] For comparison with the original descriptions given by Sommer and myself, chiefly of the common bladder-worms, I may refer to the data furnished by the following investiga-

remark, in the first place, that the male apparatus consists usually of a large number of testicular sacs, whose delicate orifices open into a seminal duct with cirrhus-pouch and cirrhus (penis). In the female apparatus we have to distinguish not only an ovary (germarium) and yolk-gland (albuminiparous gland), which co-operate in the formation of the eggs, but also two kinds of exit ducts, a vagina, which serves for the reception of the semen, and a uterus, which collects the fertilised eggs, and often contains them until the formation of the embryo. With the vagina there is often connected a receptaculum seminis, and at the beginning of the uterus, where the oviducts are connected with the posterior end of the vagina, there is yet another special organ or shell-gland (Figs. 158 and 159).

The presence of a separate yolk-gland along with the ovary is a peculiarity which the Cestodes share with numerous other flat-worms, and especially with the Trematodes. The secretion furnished by the gland surrounds the eggs, which in their state of formation possess only a thin, clear protoplasmic sheath, and thus during the whole of

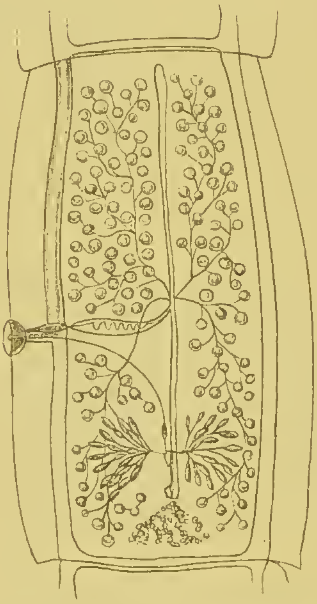


Fig. 158.—Sexual organs of *Tænia cœnurus.* (× 10.)

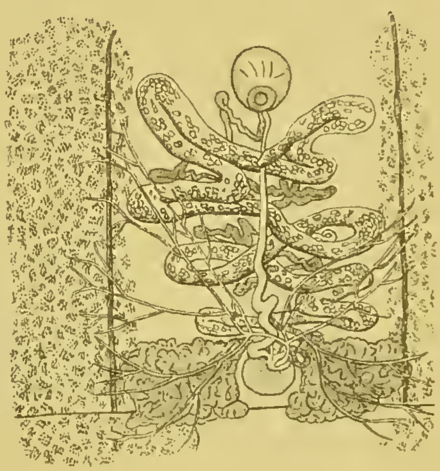


Fig. 159.—Sexual organs of *Bothriocephalus latus* (from the ventral side). (× 20.)

their sojourn in the ovary exhibit conditions which in other cases exist only for a short time, until the deposition of the granular yolk. Such

tors concerning the structure of the sexual organs in other forms of *Tænia*—Stieda (*Archiv f. Naturgesch.*, Jahrg. xxviii., p. 200, 1862), Pagenstecher (*Zeitschr. f. wiss. Zool.*, Bd. ix., p. 523, 1858), Feuereisen (*ibid.*, Bd. xviii., p. 161, 1868), v. Linstow (*Archiv f. Naturgesch.*, Jahrg. xli., p. 187, 1875), and Kahane (*loc. cit.*).

being the state of matters, we can understand how v. Siebold, to whom we owe the first discovery of this peculiar structure,[1] and his next followers (among whom I was numbered at the time of the first edition of this work) recognised in the products of the ovary only a germinal vesicle, which was then generally believed to serve, as in other animals, as a starting-point for the future egg. We need hardly add that v. Siebold's idea needs no particular refutation at the present day.

But the Cestodes have, in common with the Trematodes, not merely a double egg-forming organ, but also a double female conducting apparatus. The opinion formerly held that the so-called "uterus" of the latter took part in copulation as well as in the deposition of the eggs, was erroneous, as has since been placed beyond a doubt by the well corroborated observations of Blumberg and Stieda.[2] The same error prevailed, however, in regard to the female conducting apparatus of *Bothriocephalus* until Stieda's researches proved the existence in this case also of a special vagina beside the uterus.[3] In the Tæniadæ the simultaneous presence of vagina and uterus had indeed been long recognised, but the structure in this case seemed exceptional, since in these animals the uterus is anomalous in being destitute of an opening.

Minot considers the presence of two kinds of female conductive canals as such a characteristic and important peculiarity that he proposes to unite the Cestodes and Trematodes into one group of "*Vaginiferæ*." But, on the other hand, it ought to be remembered that a similar arrangement also occurs in other lower animals. The female butterfly, for instance, generally possesses a vagina, which is separate from the oviduct, except for a narrow duct, and opens exteriorly by a special opening near the latter—a state of affairs essentially similar to that found in the so-called "vaginiferous" Helminths.

Although united in the same body, the male and female organs of the Cestodes differ from each other, in becoming functionally capable and mature at different periods of life.

As I have long since shown, it is the male organs which first develop and attain maturity, and that at a time when the female parts are often imperfectly sketched out, so that in many cases one feels tempted (Feuereisen remarks this especially in the *Tænia setigera* of the goose) to characterise the anterior joints as exclusively male (Fig. 160, *A*). In studying the male apparatus, it is therefore

[1] "Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere," p. 146, 1848.
[2] "Ueber d. angebl. inneren Zusammenhang d. männl. u. weibl. Organe d. Trematoden," *Müller's Archiv f. Anat. u. Physiol.*, p. 31, 1871.
[3] "Ein Beitrag zur Anatomie des Bothriocephalus latus," *ibid.*, p. 194, 1864.

better to examine the younger proglottides, whose ovaries are still without eggs. In the older joints, in which copulation has taken place, and the embryos are perhaps already developed, the testicular sacs are generally empty and deserted, and sometimes have even in great measure disappeared. Even the cirrhus and cirrhus-pouch often fall into decay (Fig. 160, *B*).

This unequal development is most striking in the Tæniadæ, which, having no uterine opening, are unable to void their eggs successively, and form them indeed only during a relatively short space of time, whilst the Bothriadæ go on depositing during their whole life, as long as they remain in the intestinal canal of their host, and thus require the spermatic elements during a longer time. In this way it also becomes clear that the Bothriadæ not only continually replace the externally deposited eggs by new batches, but as time goes on collect larger and larger numbers in their uteri, which, while still in the neighbourhood of their place of formation, distinctly exhibit the characteristics of their youthful stage. On the contrary, the number of eggs in the *Tæniæ* is not increased after the transference has once taken place into the uterus. And as this transference, as already mentioned, only lasts during a definite and relatively short period, the eggs in the interior of the uterus are all of nearly the same age, and of the same or only slightly different development.[1] And this is all the more surprising in these animals as the development of their eggs goes much further than in the case of *Bothriocephalus*, and only terminates with the formation of an embryo. When the uterus is filled, the female germ-producing organs of the *Tæniæ* have fulfilled their function, just as have the testes after the filling of the seminal duct, and are then gradually destroyed by the pressure of the uterus, which becomes larger and larger during the embryonic development of the eggs. In the investigation of the generative organs in *Tænia*, the smaller "unripe" joints must evidently be examined, for in the so-called "ripe" or pregnant proglottides these parts are only slightly present, or have even entirely disappeared.

[1] Sommer declares (*loc. cit.*, p. 532) my statements, that "in the case of the *Tæniæ* the transference of the eggs into the uterus is limited to only a short space of time," and that consequently "the eggs of a uterus are always of nearly the same age, and of similar or only slightly different development," to be erroneous. He bases this assertion on the fact that the transference of the eggs in *Tænia saginata* takes place over a stretch of 300 to 400 proglottides, and that the eggs of the older proglottides in the posterior end of the uterus stem differ considerably from those found in the side branches. I have known these facts from my own experience, and for a long time, but, notwithstanding, I think I am able to support my statements. For Sommer overlooks that the matter in question was not the nature of the Tæniadæ *per se*, but the contrast between it and that of *Bothriocephalus*, and I still think that this contrast was perfectly accurately and naturally characterised in the way I put it.

As has already been mentioned, the male and female organs are differently situated with respect to the two surfaces of the tape-worm, the former belonging to the back and the other to the ventral surface. Here, too, as in the position of the sexual openings, numerous and striking differences appear, which at first sight are little in accordance with the general nature of bilateral structure. This is particularly true of the forms which have genital openings on one margin, which is the case indeed in the majority of Cestodes, and especially of *Tetrabothria*.

What was formerly said of the genital openings in the Cestodes was only true of the vaginal opening, which is the only female opening constantly present in these animals, and is always situated near the male one.[1] These two openings, which alone form what is usually called the porus genitalis of the Cestodes, vary in their position, but the uterine opening, when present, is always found on the ventral surface, and, with the exception of a few species with double uterus and double opening, lies on or near the middle line.[2] When the other genital openings are also ventrally situated, the uterine opening lies a short distance behind them, or more rarely near them.

There are thus two openings in the porus genitalis of the Cestodes, the male opening and the female vaginal opening. They lie close together, and the male one is generally above.[3] The latter only assumes a lateral situation in very short-jointed tape-worms, such as *Tænia nana* and *T. perfoliata*, and also in *Ligula* and *Schistocephalus;* and it is usually so associated with the female, that they have a short and narrow pouch in common, a general cloaca, which is clad with a thin prolongation of the investing cuticle, and, in spite of its originally small size, seems capable of considerable extension. In many species, and especially in the larger ones, a more or less marked swelling surrounds the porus, which is sometimes flat and plate-like, but often deeper, and then protrudes like a papilla on the external surface (*Tænia saginata*, &c.).

From the male opening there generally protrudes a longer or shorter thread-like process, which is known by the name of "cirrhus."

[1] The statement of von Siebold (Vergl. Anat., p. 147), that in *Triænophorus* and *Tænia ocellata* these openings were situated far from each other, since the vulva was found on the ventral surface, but the penis on the margin, probably rests upon an error. There is, indeed, no doubt that he has made a mistake in the case of *Triænophorus* at least, for the vagina is overlooked, and the uterine opening interpreted as a vulva.

[2] It is so in *Triænophorus*, whose uterine opening, according to Steudener (*Abhandl. naturf. Gesellsch. Halle*, Bd. xiii., p. 302, 1877), diverges a little towards the opposite side of the peripheral porus genitalis. It is the same in the Ligulidæ (see Kiessling).

[3] In *Tetrabothrium*, van Beneden (*loc. cit.*) describes the vaginal as above the cirrhus pouch, but this is a mistake, as the case of *Tetrarhynchus* has convinced me.

This is a copulatory organ, which is introduced into the female opening,[1] and indeed generally into that of the same joint (van Beneden, Leuckart), and being provided with a fringe of backward-directed bristles or points, is specially adapted to effect a firm union. As a rule, however, this cirrhus is not an independent organ, but the more or less independently developed anterior end of the so-called muscular "cirrhus-pouch." This is attached to the male opening, and consists of a conspicuous structure of cylindrical or ampulla-like form, which is completely surrounded as far as the point mentioned by the body-parenchyma,[2] with which it is also connected by retractor and protractor muscular fibres. In a certain sense, however, the cirrhus-pouch appears to be also a part of the seminal duct; at all events, the latter appears to be in direct continuity with it. Its internal cavity may be observed running along the whole length of the cirrhus pouch as a distinctly marked passage, with pretty thick cuticular covering; and one even feels convinced that it is only the highly developed muscular wall of this passage which forms the cirrhus-pouch, and that it only appears to be a special structure because the other far greater part of the seminal duct is destitute of this covering.

But on closer examination it is soon seen that the cirrhus-pouch does not consist of a simple layer of muscles, but rather of a muscular external wall and of an internal mass, which is partly, it is true, of a muscular nature, but consists principally of a clear connective substance. The enveloping layer exhibits fine thickly matted fibres, which sometimes run circularly, or at other times with a more diagonal course, crossing each other and forming a hollow muscle, which is evidently able powerfully to compress the interior mass. In contrast to this, the fibres of the latter have a more longitudinal

[1] Sommer doubts the existence of a special copulation in the Cestodes (*loc. cit.*, p. 507), and only admits an overflowing of the seed into the vaginal opening, which might easily be caused by the pressure of the body after the closure of the genital pore and the shutting off of the general cloaca. This, he says, he directly observed in the case of *Tænia saginata* and *T. solium*. In answer to this, I can only repeat that I have observed just as directly, and in the most distinct manner, an "*immissio penis*" (Fig. 165) in *Tænia echinococcus*, and that under circumstances which excluded the possibility of confusing it with the overflowing of spermatic masses. Besides this, it cannot be admitted that an organ, which in many species is as long as half the width of the body, and which most obviously possesses all the characteristics of a copulatory organ, should only serve its possessor as an ornament. Yet, as the structure of the cirrhus exhibits many varieties, it is quite conceivable and possible that the act of copulation is not always effected in the same way. But the above observations of van Beneden and myself are not the only ones which can be adduced against Sommer. Pagenstecher (*loc. cit.*, p. 528) has also observed the copulation in *Tetrabothrium auricula*, but in this case no self-fertilisation took place, but the penis of one joint was sunk into the vagina of another, a few joints distant.

[2] Kahane describes the cirrhus of *Tænia perfoliata* as a special organ, situated at the base of a pocket or bell-shaped cirrhus-pouch, from which it protrudes.

course, for they proceed from the rounded posterior end of the pouch, and, converging anteriorly, attach themselves ultimately to the cuticular wall of the seminal duct. In many cases this anterior part of the seminal duct is also characterised by a thinner or thicker fringe of spines situated on the cuticle. Its course is also always straight and extended, while that of the posterior part, situated at the base of the cirrhus-pouch, is generally coiled or twisted.

There can be no doubt as to the purpose of this muscular terminal apparatus. It serves to protrude the penis, which in the state of rest is more or less withdrawn, and lengthens it by the evagination of the anterior end of the seminal duct. Under the pressure of the powerfully contracting muscular pouch, the internal elastic mass reacts on the free and pliant anterior end, until a regular prolapsus results, in consequence of which the spinous fringe of the seminal ducts emerges, and its windings adapt themselves more or less to the length of the prolapsus. The retraction is accomplished by the above-described longitudinal fibres, which pass through the interior mass, and are physiologically antagonistic to the hollow peripheral muscle.

The seminal duct, or vas deferens, proceeding from the rounded posterior end of the cirrhus-pouch is destitute of special musculature. Its walls consist of a thin and extensible glassy membrane, which is a continuation of the above-mentioned firm cuticle, and lies loose in the substance of the body-parenchyma. On the exterior there is generally distinguishable a layer of clear, delicate nucleated cells, which may be interpreted as a kind of epithelium, and which, so far as one can judge from appearances, can hardly be referred to the connective-tissue corpuscles. We shall consider this afterwards, when describing the manner of development of the generative organs.

In spite of the thinness of its walls, the seminal duct is in many cases of considerable width—sometimes throughout its whole length,

FIG. 160.—Two proglottides of *Tænia setigera* from the goose (after Feuereisen). *A*, Male, and *B*, Female development. *a*, end of the vagina; *b*, receptaculum seminis; *c*, yolk-gland; *d*, ovary; *f* and *g*, seminal vesicles; *h*, testes. (× about 40.)

and sometimes only in a definite place—in the neighbourhood of the cirrhus-pouch. This is due to its contents, the spermatozoa, which accumulate in it in great numbers at the time of the male maturity,

and distend it to such an extent that one is tempted to speak of distinct sperm sacs. Sometimes straightly extended, and sometimes more or less tightly wound, the canal runs in a transverse direction (Fig. 158), or perpendicularly downwards (Fig. 159), according to the position of the porus genitalis, and ultimately breaks up into a number of thin, delicate canals, which sooner or later, and often after repeated ramification, meet the little testes, and are united with them.

The anatomical condition of these vasa efferentia is largely determined by the distribution and number of the testes, both which factors are subject to extraordinary variations. In the larger species many hundred testes (Fig. 158) are found, consisting of clear and round little bladders. These are each surrounded by a clear, structureless, glassy membrane,[1] and contain tufts of spermatozoa, or the cells in which these are formed, in different stages of development,[2] and are pretty equally distributed over the whole joint. But as the size diminishes, so does the number of the testicles. Instead of a hundred, perhaps only some dozens are then found, as in *Tænia perfoliata* (Fig. 162, *A*), where they are situated in what appear to be two rows upon the vas deferens behind the sperm sacs; or they may be reduced to smaller numbers, even down to two or three, as is especially the case in certain *Tæniæ* of birds, such as *T. setigera* (Fig. 160, *A*), and also in *T. uncinata* of the shrew-mouse (Fig. 161).

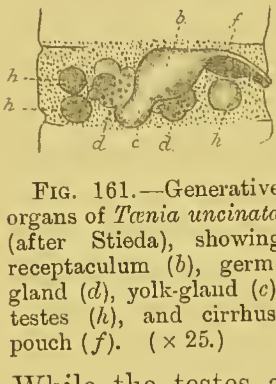


Fig. 161.—Generative organs of *Tænia uncinata* (after Stieda), showing receptaculum (*b*), germ-gland (*d*), yolk-gland (*c*), testes (*h*), and cirrhus-pouch (*f*). (× 25.)

The emptying of the testes is effected, like that of the vas deferens, by means of the muscles of the body, but the two processes are apparently accomplished by different groups. While the testes are principally subjected to the pressure of the transverse and sagittal fibres, which run through the surrounding tissue, all the more abundantly, since this is converted into a cubical meshwork by the formation of the above organs, it appears to be mainly the longitudinal and transverse fibres which act upon the vas deferens, and discharge its contents into the cirrhus-pouch.

[1] While this glassy membrane originates in the structureless connective tissue, the spermatozoa are produced by a metamorphosis of cells, which in no way differ from the young connective-tissue cells. In other words, the testes, like the other viscera of these animals, are only differentiations of the body-parenchyma (mesoderm). Thus we can understand the statement of Moniez (*Bull. Scient. dep. Nord*, p. 221, 1878) that the formation of the spermatic elements takes place in the meshes of the body-parenchyma, and not in a special organ. In the same way, he denies the presence of special vasa efferentia, and thinks that the spermatozoa make their own way through clefts previously formed in the tissue.

[2] Moniez has made the structure of these spermatozoa the subject of special investigation, *l'Institut*, July 1878.

As has been sufficiently shown by the foregoing remarks, the differences in the male apparatus are of entirely subordinate import, especially in so far as they are determined by the form and size of the proglottides. But it is in this respect quite different with the female parts, which, although also much affected in form and arrangement by the above factors, exhibit, besides, other important characteristics. These consist mainly in the structure of the yolk-gland, and are of so fundamental a nature that we have to distinguish two types of it—one which occurs in the Tæniadæ, and another in the remaining tape-worms (Bothriadæ). As both have their representatives among the human Cestodes, we shall now shortly consider them.

One of these types represented in the Tæniadæ is mainly characterised by the absence of the uterine opening, and by the small development of the yolk-gland,—characteristics which have a certain connection with each other, since they both find their explanation in the above-noted peculiarities of the breeding. The vagina, which, as we have seen, is separate from the uterus, appears as a distinctly marked narrow canal, which extends in a transverse direction from the generally marginal porus genitalis (Fig. 162), and has either a straight

Fig. 162.—Sexual organs of *Tænia perfoliata* of the horse (after Kahane). *A*, Joint in male maturity; above, cirrhus, vas deferens with sessile testes; below, the yolk-glands, uterus with shell-gland and yolk-gland, vagina with receptaculum. *B*, Female organs at the time of the transference of the eggs into the ovary. (× 15.)

course, or, as in the *Tæniæ* with extended joints (Fig. 165), curves backwards towards the middle of the joint. The posterior end enlarges into a receptaculum seminis of varying and sometimes considerable size, and is filled with semen at a time when the uterus contains as yet no eggs. The vagina itself is, on the contrary, generally empty, and its lumen is much contracted, obviously because the firm cuticle which covers it, especially in the posterior part, is very elastic, and quickly forces the introduced semen into the receptaculum. There is no muscular sheath in the vagina. The only layer found on the cuticle consists of a pretty thick epithelial layer, somewhat like that which we observed in the vas deferens.

But the posterior end of the vagina not only leads into a sperm

sac (Fig. 163, *c*), but is in more or less direct connection with the uterus. As a rule, and perhaps always (especially in the case of the *Cystotæniæ*), this union is effected by means of a special tube which I have named the "fertilising canal" (Befruchtungscanal).[1] It originates from the posterior end of the sperm sac—being indeed in some measure a continuation of it and of the vagina —and opens into the uterus after a short course. Where the latter occupies the middle line, it always opens at the posterior end, where the "fertilising canal," especially in the *Cystotæniæ*, often assumes a curved course. At the point of union with the uterus there is found a small round body, consisting of numerous unicellular glands, which from its function I have named the "shell-gland."

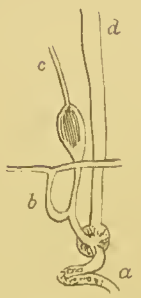


FIG. 163.—Connection between the different parts of the female generative apparatus in *Tænia cœnurus*. *a*, yolk passage; *b*, oviduct; *c*, vagina with receptaculum; *d*, uterus; *e*, fertilising canal. (× 50.)

On its way to the shell-gland the fertilising canal receives the exit canal of the ovaries, of which two are always present in the

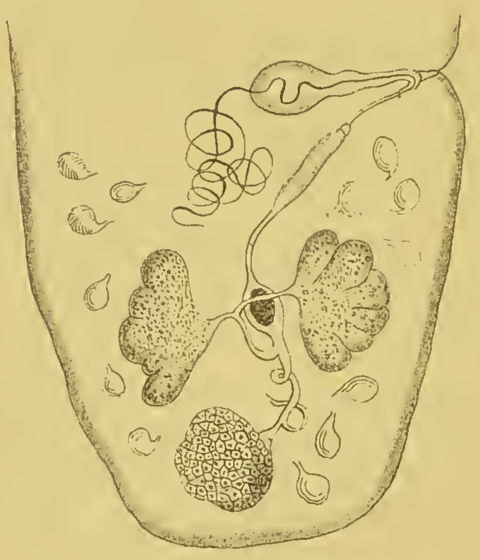


FIG. 164.—Sexual organs of *Tænia echinococcus* (penis during copulation). (× 100.)

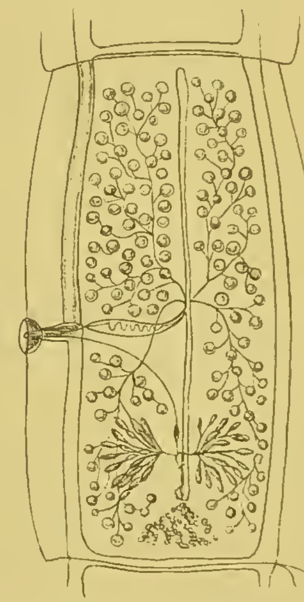


FIG. 165.—Sexual organs of *Tænia cœnurus*. (× 10.)

Tæniadæ. In the majority of cases these have the appearance of two wing-like or hand-shaped organs, which are situated about the

[1] I may take this opportunity of mentioning that I was the first to observe the connection between the different parts of the female sexual apparatus. The description given

the height of the sperm sac, and also somewhat below it, on the right and left of the middle line, and may be beautifully and distinetly brought out by injected microscopic preparations. Constructed on the type of the tubular glands, they consist, especially in the larger speeies, of numerous more or less branched tubes, which eontain the egg-cells enveloped within an extremely fine structureless membrane, in the form of clear, membraneless, little balls, with comparatively large germinal vesieles.

But it is quite different with the yolk-gland (albuminous gland, Sommer), not only because, although usually an unpaired organ, it is sometimes drawn out to the side, but because its efferent eanal opens directly into the shell-gland, into which there are also poured semen (Figs. 163, 164), eggs from the ovary, yolk, and shell material, and which possesses all the conditions necessary for the later formation of the eggs. The yolk-gland is situated near the posterior extremity of the joint, and thus below the other parts of the female apparatus. In the larger species it consists of a branched glandular body like the ovary; but in other cases it is of a simpler saccular shape. The very fine and structureless walls enelose little eells, which in the young joints often contain several nuclei, but which afterwards generally dissolve, and assume the appearance of a somewhat thick and tough glandular seeretion.

The manner in which the position and arrangement of the above shortly deseribed organs is affected by the form of the joint is well shown in the structure of *Tænia perfoliata*, which we may regard as typical representative of the short and broad-jointed Tæniadæ. It is most notieeable in the ovaries, whieh, in contrast to their usual structure, appear as two thin eanals, whieh run out from the middle line towards the edges, and are provided throughout with short unbranched

FIG. 166.—Male and female organs of *Tænia perfoliata* (after Kahane). (× 15.)

egg-follicles (Fig. 166). They have thus a remarkable resemblanee to the male secretory apparatus, which is also determined by the form of the body, and runs in the same direetion, and to pretty nearly the

in the former edition of this work is also the first complete analysis of these structures. All the more do I regret that, in opposition to the former eorrect opinion held by von Siebold, van Beneden, and myself ("Blasenbandwürmer," p. 79), I unfortunately represented the yolk-gland as the ovary, and described the real germ-gland as the yolk-gland. To any one who knows the difficulties whieh the investigator encounters at this very part, the mistake will appear pardonable. It is all the more easily committed, sinee the contents of the two glands have often a great resemblanee. Further, later observers, and particularly Stieda, Feuereisen, and v. Linstow, have made the same mistake.

same height, but does not, like the ovaries, approach the ventral, but the dorsal surface.

Lastly, as regards the uterus, it is at first, in the Tæniadæ, a simple and straight canal, which, according to the form of the body, runs in a transverse or perpendicular direction, and in the latter case its posterior end (or its middle, as in *Tænia perfoliata*, Fig. 162, *B*) is connected with the vaginal canal. Like the other portions of the female apparatus, it consists of a structureless, expansible, and elastic membrane, whose external surface exhibits the repeatedly mentioned but here specially abundant accumulated cells. Since there is also no appearance of any special muscular covering in the uterus, the expulsion of the eggs through the previously formed rupture must, of course, be effected by the pressure of the muscles of the body.

But afterwards, when the eggs are transferred into it, and accumulate in it in ever larger numbers, and of increasing size during the

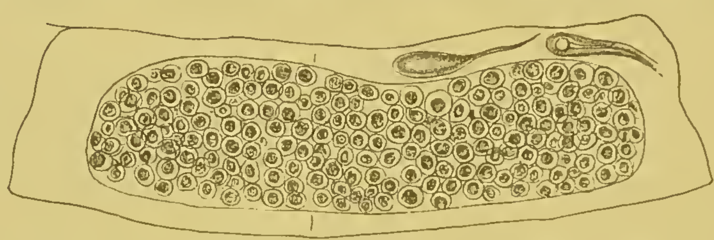


Fig. 167.—Proglottides of *Tænia nana* at maturity (× 100).

Fig. 168.—Mature joint of *Tænia perfoliata* with uterus (× 10).

development of the embryo, this primitive form of the uterus undergoes a continuous and often very striking change. In some cases it consists of a simple enlargement, often so extensive that the original linear tube becomes a bulging sac (Fig. 167), and in other cases lateral processes, varying in number and width (Fig. 168), are formed, which ultimately turn into slender and often branching twigs (Fig. 169). But such differences, however highly characteristic of the different groups and species, can only be shortly noted. Therefore I shall only observe that in some cases the uterus even breaks up into many round vesicles, containing a larger or smaller

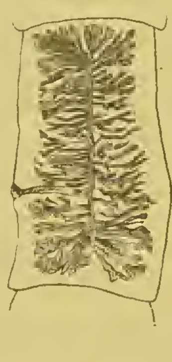


Fig. 169.—Joint of *T. saginata* (× $\frac{4}{2}$).

number of eggs. The latter are further generally enclosed in a common more or less firm envelope, as we shall afterwards see in the case of *Tænia elliptica* and others.

If, however, there be two pori genitales in every joint, the uterus always remains simple, but instead of a simple vagina, it then possesses two (each with a receptaculum). In *Tænia elliptica* (Fig. 143), *T. denticulata*, and others, each vagina has a special germ-producing organ, whilst in the "biporous" proglottides of *Tænia solium* the ovary and yolk-gland are developed as usual along with two symmetrical vaginæ (p. 279). According to Moniez, the two receptacula of *T. Giardi* (a new form found in the intestine of the sheep, and nearly related to *T. denticulata*) send each a fertilising canal to the ovary of the opposite side.[1]

The second typical form of the sexual organs is much more widely distributed among the Cestodes than the one which we have considered, and indeed apparently occurs in all the species which remain after the exclusion of the Tæniadæ (*i.e.*, in the Bothriadæ), being found in the forms where the genital pore is marginal, as well as in those where it is situated on the surface. As the former have a very general resemblance to the *Tæniæ* in regard to the structure of the male apparatus, vagina, and ovary, and as none of them are found in man, we need not give them special attention.[2] Further, their distinctive characteristics, and especially the structure of the yolk-gland and the presence of a special uterine opening,[3] will be sufficiently elucidated

[1] *Comptes rendus*, t. lxxxviii., p. 1094, 1879.

[2] Compare, regarding the sexual organs of these forms, the statements of van Beneden ("Vers Cestoides," p. 53), and of Sommer and Landois (*loc. cit.*) Moniez's recent reports (*loc. cit.*) on these structures, as specially observed in a new form, *Leuckartia*, are indeed very divergent, for he disputes the independent existence of nearly all the parts except the yolk-gland, but particularly of the uterus, shell-gland, and ovary. He thinks that, as in *Tænia*, the eggs originate in a cellular mass found in the meshwork of the parenchyma, provide themselves with yolk-granules, which reach them by ways of their own making, and lastly become surrounded by a shell. My own investigations, which had partly to do with the same objects (*Ligula*), do not lead me to agree with Moniez's interpretation and description, but, on the other hand, I do not deny (p. 312) that the sexual organs and the later formed connective substance both originate from the primarily quite undifferentiated cellular mass of the parenchyma.

[3] I may, however, expressly mention that the presence of this uterine opening has as yet only been observed in few Bothriadæ, although its general presence may be presumed from the essential uniformity in the structure of the sexual organs. I am also convinced that a similar opening is to be found in *Ligula* and *Schistocephalus*—two species, which in spite of the many differences which they exhibit in the organization of their sexual apparatus, are essentially allied to the Bothriadæ. Donnadieu's statements regarding the sexual organs of these animals (*Archiv. physiol.*, 1878), rest upon a complete misconception of their real structure: see the above-cited memoir of Kiessling. Further, if the Tæniadæ possessed a uterine opening like the Bothriadæ, it would be situated on the at present closed anterior extremity. At least it would be so in the species with a perpendicular uterus, and in those where the uterus assumes a transverse course it would presumably occupy a lateral position.

in the following descriptions. The latter, however, refer mainly to the forms with mesially situated porus, and especially to the genus *Dibothrium*, or, as it is generally called, *Bothriocephalus.*[1]

As to the male organs (Fig. 170, *A*) but little can be said. Anatomically and histologically they resemble the same organs of Tæniadæ, and indeed they only differ from them in particulars which are determined by the ventral position of the porus genitalis. Thus the vas deferens starts from the base of the cirrhus-pouch, which is perpendicularly situated upon the ventral surface, and runs down the middle of the joint, under the dorsal surface, as a tolerably wide canal, bending sometimes to the right and sometimes to the left of the middle line. Whether the bulbus musculosus, which in *Bothriocephalus latus* lies close behind the cirrhus-pouch, is of wide distribution, cannot be determined without further investigation, but one feels tempted to connect its presence with the above-mentioned position of the cirrhus-pouch, and to interpret it as a pumping apparatus, designed to remove the difficulties attendant upon the transference of the semen, with

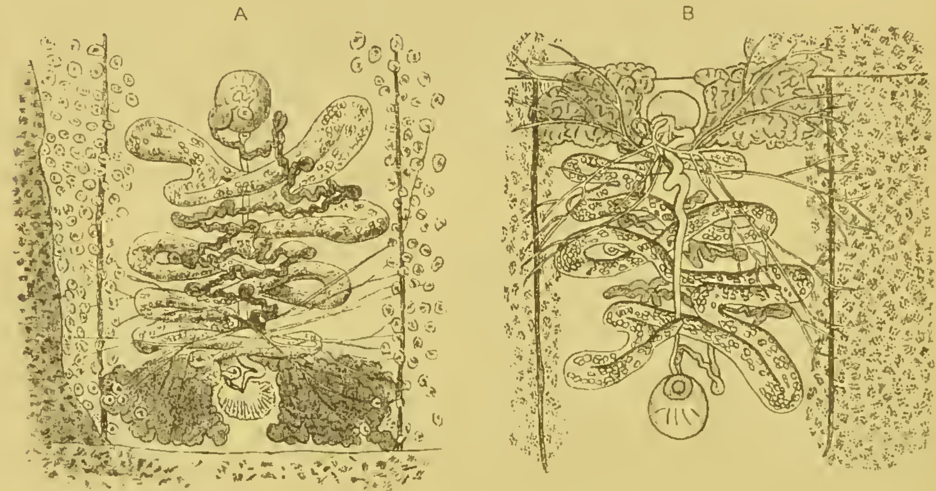


Fig. 170.—Male (*A*) and female (*B*) sexual organs of *Bothriocephalus latus.* (× 20.)

which the seminal duct is itself abundantly filled. This filling takes place exclusively at the posterior end, into which the vasa efferentia

[1] Besides Eschricht's classical work on *Bothriocephalus latus*, which we shall often have occasion to quote, it is especially to the already mentioned treatises of Stieda and of Landois and Sommer that we owe our increased knowledge of the structure of the sexual apparatus in *Bothriocephalus*. The description which I have given in the first edition of this work, although expressing even in details many of our present views, contains a number of errors. These are of course corrected in this edition, and throughout, on the strength of my own observations, which corroborate the results of Stieda and Sommer and Landois.

of both sides open. The testes are apparently always present in great numbers and pretty equally distributed over the middle layer.

The vagina and uterus (Fig. 170, *B*) have, on the whole, the same course as the seminal duct, only differing from it in so far as they lie in another plane. This is especially true of the vagina, which lies upon the ventral surface, very much as the vas deferens lies upon the dorsal surface. These three canals cover one another in their course, and this must be to a large extent the reason why the vagina—the narrowest and most insignificant of the three, in spite of its contents of semen —has remained only imperfectly known, and was often wholly overlooked till after Stieda's researches. It runs downwards in a pretty straight course, while the uterus, at least in the older joints, forms on each side a number of oval loops. These project a considerable distance towards the sides, and are all the more conspicuous since they are stuffed full of eggs, and from their dark colour stand out in sharp contrast to the other organs. Only in the narrow posterior part does the uterus exhibit less regular windings, and a more simple structure. Although the hinder portion of the vagina is not unfrequently distended into a sort of cæcum, no proper sperm-pouch seems to be present, the whole vagina being, as we have mentioned, usually filled with semen.

At the connection of the vagina with the uterus there is also a fertilising canal, which ends in a shell-gland—the so-called "coiled gland"—of which the real nature was first understood by Stieda, and which I erroneously held to be the ovary. This canal, as in the Tæniadæ, receives the efferent canals of the proper reproductive organs. Although there are instances of a more or less marked simplification (*Caryophyllæus*) the ovary is, as a rule, of a hand-like or wing-shaped structure, and, except in *Ligula*, generally exhibits the already familiar symmetrical arrangement. This is the structure which I formerly identified in *Bothriocephalas* and in the *Tæniæ* as the yolk-gland, which is, however, really represented by the organs described by Eschricht as ventral and dorsal granules. These yolk-glands are, indeed, the most striking and important characteristics of the Bothriadæ, not only on account of their size, but because, unlike the other sexual parts, they belong to cortical layers of the body. In many species they run down the sides of the joint in the form of a pretty large cæcal tube, abundantly provided with lateral protuberances, especially on the outer side. They open ultimately into the vaginal canal by means of an efferent canal, which runs transversely from the middle line, and close beside the shell-gland. They thus exhibit conditions similar to those which we shall afterwards find in the Trematodes—conditions, moreover, which may undergo many

modifications by the more or less independent development of the cæcal tube. This is especially true of *Bothriocephalus* (*sensu stricto*) and *Ligula*, in which these lateral tubes are broken up into a large number of round or oval sacs (Fig. 170), which insinuate themselves between the so-called "subcuticula" and the longitudinal muscles, and when in their usual position, are found not only in the borders, but also over a great part of the lateral portions of both surfaces. Their contents consist mainly of the somewhat large and coarse-grained yolk-cells. These pass into the fertilising canal by means of a branching system (Eschricht's "yellow canals)," and finally in the shell-gland, or in the commencement of the uterus, become enclosed in a firm shell, along with a pale and membraneless ovarian egg.

At first sight the differences between these yolk-glands of the *Bothriocephali* and the above-described corresponding organ of the Tæniadæ appears so striking that one feels inclined to adopt the view of Sommer, who calls the latter an "albuminous gland," and distinguishes it from the "yolk-gland" of the other Cestodes. And this seems all the more likely since the nature of the secretions is different, for while the products of the yolk-gland are granular cells, the albuminous gland yields a tough and almost homogeneous fluid. Yet this fact is of little significance, for many differences are also found in the secretion yielded by the yolk-gland, which in the latter instance are dependent on the degree and nature of the breaking up of the cells yielded by the glandular wall. In considering these conditions it must not be forgotten that the structures in question do not produce an ordinary yolk, but an envelope for the egg, which, however, like the granular yolk, furnishes nutriment for the embryo, but in its relation to the true egg more nearly resembles the albumen of the bird's egg. For this reason it has often been proposed (especially by Reichert) to change the name "yolk-gland" for "albumen gland."

Albumen gland and yolk-gland in these worms are, however, by no means to be regarded as physiological contrasts, or at least they are not so different as might perhaps have been supposed; and it seems to me also, that in the conditions existing in the Cestodes there is hardly any difference morphologically between the organs in question.

In support of this statement, I may refer to the structure of the yolk-gland in *Caryophyllæus*, which, besides the two posteriorly situated lateral tubes, also exhibits a middle portion, corresponding in position and arrangement to the albumen-gland of the Tæniadæ. If we suppose the lateral organs to disappear—and this supposition is justified to some extent by the smaller yolk requirements of the Tæniadæ—then the only difference left is that in *Caryophyllæus* the remaining structure belongs to the cortical layer, but in the Tæniadæ

to the middle layer. Yet this is apparently a necessary consequence of the fact that the middle layer of the jointed tape-worms passes continuously, as we have seen, throughout the whole length of the body.

Consequently I see not the slightest ground for regarding the yolk-gland of the *Bothriocephali* as quite different from that of the Tæniadæ, nor for describing it by another name, which almost necessarily leads to a different conception of it.

But without supposing a different nature of the yolk-glands, there are considerable differences between the Tæniadæ and the other Cestodes in the structure of the sexual organs. These find their expression in the nature of the eggs, which originate from the operation of the germ-glands. In the *Bothriocephali* they are at first of a relatively large size, and are composed of a thin shell, generally of oval shape, which encloses the ovarian egg, surrounded by the granular yolk-cells. In contrast to these, the generative products of the Tæniadæ, which are first fully formed in the end of the uterus, consist of very small round balls with a clear and almost non-granular yolk, and with only a thin and loose covering, which in many of the larger species is prolonged at one (*Tænia marginata*) or at both (*T. saginata*) ends into a kind of tail.

FIG. 171.—Egg of *Bothriocephalus latus*, showing yolk-cells and shell. (× 300.)

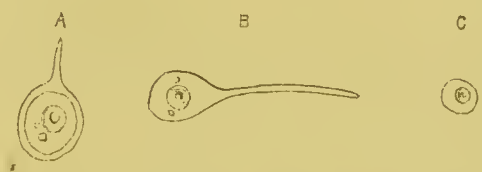


FIG. 172.—Recently formed egg of *Tænia marginata* (*A*, *B*) and *T. elliptica* (*C*). (× 600.)

But if we wish to see the latter in their above depicted primitive form, it is necessary to observe the young, or, as they are generally

FIG. 173.—Embryo containing egg, *A*, of *Tænia solium* (without yolk-skin), *B*, of *T. nymphæa*. (× 400.)

called, immature joints, in which the uterus is still of its original shape, or in which the lateral branches are just beginning to be formed. In the older and so-called mature joints a peculiar alteration has taken

place in these eggs, for they have become large and generally round balls with a more or less firm shell, which contains a clear globule, with six slightly bent hooks (Fig. 173) arranged in pairs anteriorly and laterally. These bodies are the embryos, first accurately observed and described by v. Siebold.

During the growth of the joint in the *Tæniæ*, the embryonic development also progresses. The older mature joints, whose uterus often appears of a rusty-brown colour from the contained eggs, have gradually become pregnant animals.

The size of the embryos of *Tænia* and of their hooks varies greatly in the different species. This is especially true of the hooks, which often attain a disproportionate development, and become so long that they penetrate the greater part of the embryonic body. And even in the same embryo there may be differences in the degree and manner of their curvature. In general, however, the structure of the hooks has a great resemblance to that of the adult *Tæniæ*, except that as the root has a very straight course, the general form is more linear.

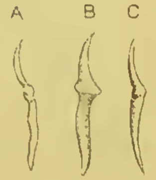


FIG. 174. — Embryonal hooklet of *Tænia crateriformis*, from a bird. *A*, a middle hooklet; *B* and *C*, anterior and posterior hooklets. (× 700, after v. Siebold.)

In some species, such as the *Tæniæ* of birds, these hooks often exhibit a distinct motion. They approach with their free points a common apex, and in their motion from it diverge downwards, the two side pairs moving almost simultaneously in the lateral plane, and the middle pair somewhat later in a median direction.

The shell which surrounds these embryos, without, however, lying closely upon them, is sometimes thin and smooth, and is sometimes also furnished with granules or with a number of little perpendicular rods close beside each other, as is especially the case in the larger *Cystotæniæ* (Fig. 173, *A*). Nor is this always the only covering of the embryos. In many species a second and occasionally even a third skin has been found, both of peculiar and striking form.[1] But even in cases where these extra coverings around the shell are wanting, as in the larger *Tæniæ* of man and carnivorous mammals, one sometimes notices, especially if the egg be cautiously emptied, an albuminous envelope bordered by membrane.

FIG. 175.—Egg of *Tænia nana* occurring in man, *A*; and of *T. solium*, *B*, with shell and yolk skin. (× 400.)

[1] In this connection see the statements of v. Siebold regarding the egg-shell and form of the eggs in the *Tæniæ* in Burdach's "Physiologie," 2 Aufl., Bd. ii., p. 203, 1828-35.

Besides the shelled embryo, this generally encloses a number of shining fatty granules which are often collected in large clusters. In older eggs, this albuminous layer is often completely lost, so that the thick shell is then the only embryonal envelope.

The difference between these embryo-containing eggs and the original contents of the uterus is so striking, that it is right to inquire into the processes by which the latter are transformed into the former. This investigation is, however, anything but easy, especially in the large-hooked *Tœniœ,* whose eggs can be isolated only with difficulty. On the strength of my later observations, I am obliged to modify in many ways the statements which I formerly made regarding the embryonic development of the *Tœniœ,* which were, however, the first published.[1]

I recall, in the first place, that the eggs on which our description is to be based are not simple ovarian eggs, but consist of these, plus an albuminous enveloping substance, which is covered exteriorly by a thin and transparent skin—the primitive shell-membrane. The whole structure has the appearance of a more or less spherical ball of about 0·03 mm., which at first sight one might easily take for a simple cell with a large vesicular nucleus (0·018 mm.). Only gradually does one perceive that the nucleus is surrounded by a narrow, membraneless coating of protoplasm, which, with its contents, is really the ovarian egg. Besides the latter, the enveloping substance in *T. solium* and its relatives generally contains one or two shining fatty bodies of varying size (up to 0·01 mm.), and of a usually homogeneous but sometimes granular nature. Sommer, who describes the bodies as accessory yolk-granules, thinks that they originate directly in the ovary; and it is true one sometimes finds in it granules similar to, though hardly identical with, those occurring in the protoplasmic envelope.

As everywhere, the embryonic development of the *Tœniœ* is effected by a division of cells, by a process which seems to associate itself primarily with the persistent and apparently unaltered germinal vesicles. But on account of the small size of the developing mass, and the clear nature of the enveloping protoplasm, this division assumes, especially at first, a very unusual appearance, which easily leads to a wrong conception of it, and which indeed, so long as I was ignorant of the yolk-coating of the ovarian egg, led me to imagine a formation of daughter-cells in the interior of the germinal vesicle. On the whole,

[1] "Blasenbandwürmer," p. 14, and the first German edition of this work, Bd. i., p. 184. See also the descriptions of the younger van Beneden in his "Recherches sur la composition et la signification de l'œuf," p. 51: Brussels, 1870 (*Mém. couronn. Acad. Belg.*, 1868); as also Moniez, *Comptes rendus*, Nov. 1877, and *Bull. sei. dep. du Nord.*, t.x., p. 227, 1879.

the process of division takes place, at least at first, somewhat regularly. The first two divided globules again break up into two pale nucleated balls of equal size, which is of course less than that of the former. When the division has gone further, the segmentation masses collect together, and round themselves off into a spherical body — the so-called "mulberry mass" (morula). During these changes the egg has grown to a considerable size, so that the segmented mass alone is larger than the whole mass formerly was.

One might suppose that this mass of balls changed directly into the later embryo after continuous growth and diminution of its cells, and after the formation of the hooks and shell. But the development does not take place quite so simply. Van Beneden and Moniez have both observed that in certain species (*Tænia bacillaris*, *T. expansa*) a peripheral layer of cells is first found in the embryonic body, whose elements divide more rapidly, and assume a brighter appearance, than is the case in the other forms. Although at first in close contact with the embryonic body, this cell-layer gradually separates from it. A cavity is left between the two, at first only insignificant, but rapidly attaining a considerable size, and containing a clear fluid. For a time the cells are distinctly visible around this space, but afterwards they undergo a degenerative process, in consequence of which they assume a more or less granular nature, lose their former boundaries, and finally disappear. During these modifications the other cell-mass has continued its development. The cells have become smaller, and are so closely packed that they can hardly be recognised as such. In consequence of this the embryonic body has contracted into less bulk. Its boundary has become more distinct, and very soon appears very like a special envelope of homogeneous nature, which becomes gradually thicker, and raises itself like a mantle from the under layer. Not unfrequently (*Tænia bacillaris*, &c.) a second and third envelope appear in addition to this first one. They all originate as excretions from the embryonic body, in the same manner as the so-called egg-shells of *Echinorhynchus*.[1]

Yet it cannot be doubted that the enclosed spherical body is really the embryo. This is evident not only from its developmental history, but perhaps still more clearly from the rapid appearance of the characteristic embryonic hooks.

It is thus quite inadmissible to compare the firm envelope surrounding the embryo in the *Tæniæ* with the egg-shell of the *Bothriocephali*, which is from the first present in the uterus, and contains not only the embryo but also the yolk. The egg-shell is represented in this case by the outer membranous boundary of the

[1] First German edition of this work, p. 805.

albuminous mass, which takes the place of the yolk, by a structure which in certain Tæniadæ also gradually assumes a firm consistence. Regarding the structure of the horn-shaped or thread-like appendages, we have only a single observation of E. van Beneden's to go upon, according to which they are protruded subsequently during the division of the yolk. The statement rests upon the examination of *Tænia bacillaris*, which, however, differs in so far that the horns are drawn back during the growth of the embryo, and leave no trace of their presence in the mature eggs. In other cases even the newly formed egg is provided with these appendages. So it is at least in the larger *Cystotæniæ;* but the appendages vary greatly in individual cases, both as to number and mode of occurrence.[1] I find them most constantly in *Tænia saginata* and *T. marginata* (in the latter oftener one than two), but comparatively seldom in *T. serrata.* They can also be sometimes demonstrated in the younger eggs of *T. elliptica*, where again they usually occur singly. I think that they probably originate when the transference into the uterus takes place, and in a purely mechanical manner, by drawing out into threads the secretion supplied by the shell-gland.

As has long been observed in the case of *T. elliptica*, certain other alterations take place in the eggs of *Tæniæ*, after the complete maturity of the embryos, for they are collected in groups and surrounded by a firm common envelope (p. 317). The groups always correspond to the contents of a uterine branch, from the walls of which the enveloping mass is distinguished as an originally clear granular substance. The same may be observed in *T. litterata*, except that in this case the simply tubular uterus envelops all its egg-masses within a single capsule.

What we have hitherto said regarding the embryonic development of the Tæniadæ is based primarily and specially on observations made by van Beneden and Moniez in certain smaller species. In the species of *Cystotæniæ* which I have specially investigated with regard to these processes, the state of matters is somewhat different, although generally similar, so that it looks as though there might be many modifications in this respect, with which we are as yet only slightly acquainted.[2]

The first phases of the development, before the fourfold division of the eggs, exhibit, it is true, no peculiarities. The yolk-balls are pale cells of about 0·013 mm. with a large vesicular nucleus. They

[1] I owe my first acquaintance with these structures to a communication from my honoured friend E. van Beneden, who discovered them in the eggs of *Tænia saginata.*

[2] [E. van Beneden has recently made this process the subject of a thorough investigation, "Recherches sur la developpement embryonaire de quelques Ténias," *Archiv. d. Biol.*, t. ii., pp. 183-210, 1881.—R. L.]

occupy the largest space in the egg (0·03 mm.), and are surrounded by a fine granular substance, in which some coarser shining grains of a fatty nature are generally observed. But afterwards the yolk-cells alter, larger and smaller ones (0·007 mm.) can be distinguished, and as the former usually occur in threes, the latter probably originate from one of the four previous balls. And further, it is only those smaller cells which produce the body of the embryo. They multiply without losing perceptibly in size, and gradually collect into a spherical cluster near the large cells, but this mass is larger (0·02 mm.) than the one formerly found within the pale shell-membrane. The vesicular nucleus has a diameter of 0·08-0·1 mm., and a distinctly defined nucleolus. In some cases four or five cells are found instead of three, and it appears as though one of

FIG. 176.—Embryonic development of *Tænia serrata* (*A*), and *T. marginata* (*B*); *a*, eggs before segmentation. (× 550.)

the smaller cells sometimes detached itself from the rest and formed a covering-cell. We can hardly doubt that these larger cells, in spite of their peculiar origin and smaller numbers, are comparable to the already mentioned cell-sheath of other species, for, like it, they do not take the slightest part in the formation of the embryo, but are permanently present outside it in the surrounding shell. The latter originates in the form of a very delicate and smooth cuticle, as soon as the embryo has attained a size of about 0·025 mm., and has exchanged the former cellular structure for an almost homogeneous appearance. The rod-like fringe only makes its appearance gradually by the growth of protuberances upon the external surface. As the

external egg membrane has by this time increased to about 0·06 mm., a considerable space is left between it and the fringe, and this is occupied by the covering-cells, which have also increased in size and proportion to the egg, and are generally so closely packed together, that they are flattened at their points of contact. The original albumen has gradually contracted into the so-called "granular mass." This generally assumes a spherical form, and inserts itself here and there between the covering-cells, and during the growth of the embryo gradually deposits within itself a number of coarse shining granules and fat-like drops.

After a long stay in the ovary, the covering cells not unfrequently lose their external boundary and are destroyed. Their contents have generally previously assumed a finely granular nature, and in this form can usually be demonstrated for a time lying round the embryo with its vesicular nuclei. This is especially the case in *Tænia serrata*, whose covering cells are very considerably smaller than those of *T. marginata* and *T. saginata*.

The first indications of the embryonic hooks in *Tænia solium* and the related forms appear after the formation of the egg-shell, and at about the same time at which the first protuberances are observed upon the shell. They are at first little points, situated on the outer surface of the embryo, which is covered by a soft skin; and, like the hooks of the tape-worm, they become independent organs, only by the growth and development of the radical process.

Histologically, the adult embryo exhibits only a slight advance upon its former state. It apparently consists of a uniform, clear substance, in which one can distinguish at most only a number of granular deposits and fatty drops.

And this is true not only of the *Tæniæ*, but of the majority of the Bothriadæ, whose embryos have notably a similar form and armature. Only in the embryos of *Bothriocephalus latus* do I find a greater differentiation, for in this case there are not only distinct fibrous bands, which are attached to the roots of the hooks and move the latter, but also four roundish groups of cells embedded in the body, as will afterwards be more particularly described.

FIG. 177.—Ciliated embryo of *Bothriocephalus latus*. (× 500.)

The embryos of the Bothriadæ exhibit many other peculiarities in addition to these, both in origin, differentiation, and mode of life.

In regard to their mode of origin, the rule is[1] that the embryos are not developed inside the mother's body, as in the *Tæniæ*, but outside it, and often so slowly that weeks and months elapse between the laying of the egg and the time when they attain their definite structure. Being abundantly provided with granular yolk, the eggs of the *Bothriocephali* by no means require during their development that continuous supply of nourishment necessary for the less favoured *Tæniæ*.

But not only do the embryos generally develop in free life, but they usually break forth from the egg on the attainment of maturity, and swim about for a time in water by means of a ciliated mantle, until they begin their future parasitism by migration into a living creature.

The possession of the ciliated apparatus is indeed the most important and striking peculiarity of these embryos. We have observed it not only in the different species of *Bothriocephalus*, but in *Triænophorus*, *Ligula*, *Schistocephalus*, &c., and may thus presume that it is widely distributed in the allied species. The cilia are generally of considerable length, and are based upon a firm cuticular membrane, which is at some distance from the embryonic body. In young embryos (Fig. 177) the space is occupied by a layer of clear and relatively large cells of an almost bubble-like appearance, which have between them numerous sharply defined granules with strong refractive power. Older embryos exhibit only the latter, the place of the cells being occupied by a clear fluid.

Fig. 178.—Embryonic development of *Bothriocephalus salmonis* (after Kölliker). (× 300.)

This mantle occurs, however, not only in the roving embryos, but also in those which, like the *Tæniæ*, remain in the egg, and are thus of course only adapted for passive migration. We have therefore good reason to consider its presence as an almost universal characteristic of the Bothriadæ.[2] Yet it will hardly surprise us to learn, from the de-

[1] See on this subject the comparisons of v. Willemoes-Suhm, *Zeitschr. f. wiss. Zool.*, Bd. xxiii., p. 345, 1873.

[2] According to v. Siebold, there are, however, some exceptions in regard to this. See Willemoes-Suhm, *Zeitschr. f. wiss. Zool.*, Bd. xxiii., p. 344, 1873.

velopmental history, that this mantle-like structure is nothing else than the further development of that same peripheral cell layer, with which we are already familar in the embryos of the Tæniadæ.

What we know regarding the embryonic development of the *Bothriocephali* is due mainly to the investigations of Kölliker[1] and Meeznikoff,[2] which both refer to *Bothriocephalus proboscideus* (*B. salmonis*), whose embryos are produced in the mother, and whose other conditions, in spite of the divergent nature of the ovary, agree in all important respects with the embryonic history of the Tæniadæ.

In the Bothriadæ also it is only the germ-cell (germinal vesicle of Kölliker) which forms the embryo; the granular yolk-mass has no more direct share in its formation than had the more albuminoid matter of the *Tæniæ*. A spherical mass of cells results from a complete and regular segmentation. This becomes differentiated into a central nucleus and a peripheral layer, as we have seen in some *Tæniæ*. This peripheral layer becomes the above-mentioned embryonic envelope, which is destitute of cilia in *Bothriocephalus proboscideus*, but is nevertheless homologous with the similarly originated ciliated covering of *B. latus*. During the transformation of the nucleus into the body of the embryo this layer loses (according to Mecznikoff) its early cellular structure, and becomes a simple cuticular membrane enclosing the embryo.

As to the comparative embryology of this peripheral layer, we can only liken it to the ectoderm. This ectoderm, however, is never retained in later life. Even the species with a ciliated coating are stripped of it as soon as they migrate into their host. Thus we conclude that the tape-worms have no ectoderm—a conclusion to which we were formerly led by histological considerations (p. 289), which forced us to deny the existence of any true subcuticula.

The statement of the older van Beneden, that some Bothriadæ liberate their eggs in the Scolex form, is utterly without foundation, as is also the assertion that the embryos are in some cases without hooklets. We have indeed come to know of a form in the genus *Amphiline* in which ten hooks are present,[3] instead of the usual six, or the four which occasionally occur in Bothriadæ. It is, however, doubtful whether these forms ought to be referred to the Cestodes (p. 268). Yet it is interesting to note that even among the genuine representatives of the Cestodes embryos are sometimes found which have more than the normal six hooks. Thus Heller mentions instances of embryos of *Tænia saginata* with twelve, sixteen, and even thirty-two hooklets, some of

[1] *Müller's Archiv f. Anat. u. Physiol.*, p. 91, 1843.
[2] *Bull. Acad. impér. St. Pétersbourg*, t. xiii., p. 290, 1869.
[3] Salensky, *Zeitschr. f. wiss. Zool.*, Bd. xxiv., p. 291, 1874.

which were perfectly developed, but others appeared only as short blunt protuberances.[1] Moniez also speaks of tape-worm embryos with twelve hooks. I have myself seen such cases in *T. saginata* and *T. elliptica*, and Professor Ramsay-Wright has showed me, in my laboratory here, embryos with ten and even twenty-four hooks. The embryos are considerably larger than usual, some twice as large, and they bear their hooks in groups of about six on only one-half of the body.

The statement of O. Schmidt, lately reasserted by Küchenmeister, that the six-hooked embryos of the *Tænia dispar* occurring in the common frog are the result of an asexual reproduction[2] is quite erroneous; it is by no means difficult to demonstrate the existence of their generative organs.

The Development of Cestodes.

G. Wagener, "Die Entwickelung der Cestoden," *Nova Acta Acad. Cæs. Leop.-Carol.*, Bd. xxiv., Suppl. 1854; also Breslau, 1854.

R. Leuckart, "Die Blasenbandwürmer und ihre Entwickelung," Giessen, 1856.

Moniez, "Sur les Cysticerques," *Bull. sci. dep. Nord*, t. x., p. 284, 1879.

The above account of the formation of Cestode embryos has shown us that the young brood has not the least resemblance to the adult forms. The young embryos (Fig. 179) are microscopic balls, with usually six apical hooks, and differ widely from the tape-worm, both in shape and size. Between these two extremes we find a long series of wonderful metamorphoses.

Thirty years ago the further development of these embryos was wholly unknown. Dujardin supposed that they were liberated in the intestine of their host, that they passed by simple metamorphosis into the so-called "head," and afterwards, by forming joints, became the familiar tape-worm.[3] Even v. Siebold seemed at first[4] inclined to suppose that the six-hooked embryos passed directly into the subsequent tape-worm, and only opposed Dujardin by urging that this change could hardly take place in the original habitat of the mother-animal, "since the young brood was so seldom found near the Cestodes." The change

FIG 179.—Embryo of *Tænia*. (× 100.)

[1] Ziemssen's "Handb. d. sp. Path. u. Ther.," Art. "Darmschmarotzer," Bd. vii., 2, p. 600; Eng. Transl., "Cyclop. Pract. Med." vol. vii., London, 1877.

[2] *Zeitschr. f. d. gesammt. Naturwiss.*, Bd. v., 1855.

[3] *Ann. Sci. nat.*, t. xx., p. 341, 1843; or, "Hist. nat. des Helminthes," pp. 545, 633, 1845.

[4] Art. "Parasiten" in Wagner's "Handwörterbuch der Physiologie," Bd. ii, p. 673, Brunswick, 1843.

must therefore presuppose an emigration from the original host, and a transference to another victim. Afterwards v. Siebold declared that the embryo took the form of a tape-worm head "outside the intestine of the vertebrate host," and subsequently gained a new home. He gives no hint, however, as to the manner of the metamorphosis. In fact there were no direct results of observation to go upon; all the statements were more or less plausible inductions.

Von Siebold's opinion received its first actual corroboration by an observation of Stein.[1] He found in the body-cavity of *Tenebrio molitor* and its larvæ numerous cysts, which exhibited a tape-worm-like head enclosed in a bladder. This had obviously resulted from the metamorphosis of the six-hooked embryo, as the six hooks still adhering plainly indicated. In some cysts there was only a simple roundish body, without a tape-worm head; in others the formation of the latter could be seen going on within this body. As to the origin of the tape-worms,[2] it could not be doubted that the *Tenebrio* had devoured tape-worm eggs, whose enclosed embryos had been liberated by the digestion of the egg-shell, and had wandered through the intestinal wall into the body-cavity, where they had lost their hooks, become encapsuled, and produced the tape-worm head.

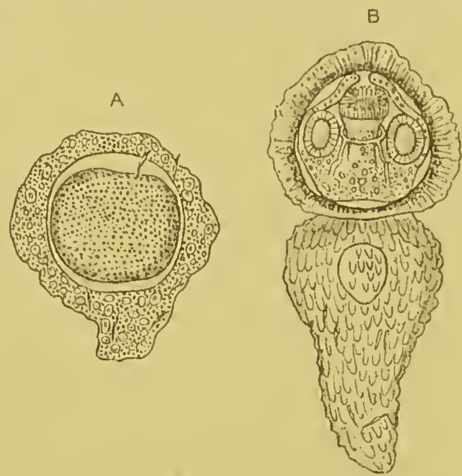


FIG. 180.—Encapsuled tape-worm embryo (*A*), and the resulting cystic worm, from *Tenebrio molitor* (× 100). (After Stein.)

Before the publication of these researches our knowledge of the development of the tape-worms had been further increased by Küchenmeister's proof that the bladder-worm of the rabbit (*Cysticercus pisiformis*) became a tape-worm (*Tænia*) in the intestine of the dog.[3]

The interest excited by this report was all the more intense since it was the first instance of a "feeding" experiment. This result had been attained by experiment, and it was speedily corroborated

[1] "Ueber den Generationswechsel der Cestoden;" *Zeitschr. f. wiss. Zool.*, Bd. ii., p. 210, 1850. "Beiträge zur Entwickelungsgesch. d. Eingeweidewürmer," *ibid.*, Bd. iv. p. 205, 1852.

[2] Probably these were the larvæ of a *Tænia* occurring in its adult form in the mouse (*Tænia murina*).

[3] *Günsburg's Zeitschr. f. klin. Vorträge*, p. 240, 1851.

and extended both by Küchenmeister[1] and by v. Siebold[2] and his school.

After these experiments it could no longer be doubted that the bladder-worms stood in definite genetic relations with tape-worms, and particularly with *Tæniæ.*

In order to appreciate the full import of this discovery, we must remember that since the time of Zeder and Rudolphi the cystic worms were commonly regarded as representatives of a special group of Helminths—the *Cystici.* It was of course known that these bladder-worms exactly resembled *Tæniæ* in the formation of their head, but the presence of a water-bladder, instead of a ribbon-like jointed body, was considered distinctive. It was this same characteristic which had concealed the true, or even the animal, nature of these organisms till towards the end of the seventeenth century, when the researches of Hartmann, Tyson, and Malpighi showed that it was no longer possible to regard them as simple hydatids.[3] Their occurrence in parenchymatous organs seemed also a sufficient reason for separating them from the tape-worms, to which they had been already referred by Pallas and Göze.[4] As to the absence of sexual organs in these cystic worms, that was hardly a difficulty. The calcareous bodies (p. 281) were in fact often regarded as eggs, and when the true state of the case was noticed, it was only another proof of the *generatio æquivoca.*

The result of Küchenmeister's experiments, though new, and surprising to the majority of physicians and zoologists, was yet not altogether unforeseen. Dujardin and v. Siebold had already advanced the supposition that the bladder-worms were not independent animals, but only developmental stages of *Tæniæ.*[5] Both supposed that the cystic worms were developed out of tape-worm germs which had reached the body-parenchyma, instead of only the alimentary canal of their host, and had, in consequence of the unwonted environment, become abnormally modified. Von Siebold especially supported this theory of the degeneration of tape-worms into bladder-worms.[6] The tape-

[1] "Ueber die Umwandlung d. Finnen in Tænien," *Prager Vierteljahrsschr.*, 1852.

[2] "Ueber die Verwandlung des Cysticercus pisiformis in Tænia serrata," *Zeitschr. f. wiss. Zool.*, Bd. iv., p. 400, 1852; and as to the metamorphosis of *Echinococcus*-brood into *Tæniæ*, *ibid.*, p. 409. (Lewald, "De cysticercorum in tænias metamorphosi," Dissert. inaug. Wratislav, 1852.)

[3] See, in greater detail, Leuckart, *loc. cit.*, pp. 1-27, &c.

[4] In his group of tape-worms Göze distinguished the *Tæniæ intestinales* inhabiting the intestine, and the *Tæniæ viscerales* occurring elsewhere. Others united the cystic worms to the other *Tæniæ* under the title *Tæniæ vesiculares.*

[5] In the second edition of his work ("Parasiten," p. 60, note), Küchenmeister underrates v. Siebold's share in the solution of the problem in a way which is, to every unprejudiced critic, utterly unfair, and he accompanies it with the unparaleled assertion (p. 163, note) that "no one has so grievously offended in the study of the Cestodes" as the "Professor of Zoology"—strictly Professor of Anatomy and Physiology—Rudolphi.

[6] See especially *Zeitschr. f. wiss. Zool.*, Bd. ii., p. 200, 1850.

worm heads which the latter possess form an appendage, but on this strange soil this gets changed by "dropsy" into a bladder.

Von Siebold gave his theories special point and weight by taking a special case of resemblance, instead of merely dilating on the general similarity; he emphasised the likeness between the head of the cystic worm infesting the mouse (*Cysticercus fasciolaris*) and the tape-worm of the cat (*Tænia crassicollis*), a comparison which had been previously expressly made by Pallas and Göze.[1] "Some individuals of the brood of *Tænia crassicollis*," he says, "go astray in the rodents, and degenerate into *Cysticercus fasciolaris;* but when their hosts are eaten by cats, and the worms are thus transplanted to their fit soil, they cast off their degenerate joints, and, returning to the normal form of *Tænia crassicollis,* become sexually mature."

To this theory v. Siebold clung all the more firmly when he found Küchenmeister's results confirmed by his own experiments.

In the changes undergone by the bladder-worm after their transmission into the intestinal canal,[2] he recognised no normal metamorphosis, but only the remedying of a previous abnormality. When the bladder-worms had altered their form in their new environment he called them "healthy," and thought that there were only certain forms which could pass through such fates to the tape-worm stage.

I must confess that I shared v. Siebold's theory for a while.[3] I was unfortunately as little aware as v. Siebold of the beautiful observations which Göze had made on the development of the cystic worms, and especially of that form found in the mouse, which was the more unfortunate since these observations were in reality decisive on the point in question, and gave a direct proof, not of the pre-existence of the head, but of the bladder. "The first thing," said Göze,[4] "to

[1] See Pallas, "Miscell. Zoolog.," p. 170, and *Neue nordische Beiträge*, Bd. i., p. 82; Göze, *loc. cit.*, pp. 222, 304. The latter speaks as follows:—"In size, shape, and structure, the head of the *Tænia serrata felina* (= *T. crassicollis*) is wholly identical with the head of the jointed bladder tape-worm from the liver of the mouse, for the latter also has no neck, but has its head directly contiguous with the first joint. But why these two forms are so similar in the structure of their head, and yet so different in other respects—who can tell?"

[2] *Zeitschr. f. wiss. Zool.*, Bd. iv., p. 407, 1852.

[3] "Beobachtungen und Reflexionen über die Naturgeschichte der Blasenwürmer," *Archiv f. Naturgesch.*, Jahrg. xiv., Bd. i., p. 7, 1848. According to Küchenmeister ("Parasiten," 2d ed., p. 19), I held, even in 1857, that the grouping of the *Cystici* along with the tape-worms was entirely unwarrantable; nay, "I then had no idea of the systematic relation of the two forms." These assertions, dogmatic as they sound, only show that Küchenmeister's literary-historical studies are not less superficial than his anatomical and embryological ones. I am in no way responsible for van der Hoeven's "Handbook of Zoology," nor for the translation of the first volume which appeared in 1851, on which Küchenmeister has relied for the truth of his statements.

[4] "Versuch einer Naturgeschichte der Eingeweidewürmer," p. 245, 1782.

appear in the development of the cystic worm from the egg is the caudal bladder." The so-called head rises subsequently, "invaginated" in the interior of the bladder, "like a candle within a lantern." We have to thank G. Wagener[1] for having called attention to these forgotten researches, and for having confirmed them by observations of his own.

Even v. Siebold found himself compelled to abandon the idea that the formation of the bladder was a secondary and abnormal process. This was due much less to Küchenmeister's polemic[2] against the theory of degenerate and strayed worms than to the above observations on the encysted tape-worms of *Tenebrio*, whose resemblance to the bladder-worms was so great that even Stein declared the *Cysticerci* to be nothing else than the second post-embryonic stage of certain *Tæniæ*. Correct as this statement was, Stein could not perfectly escape the influence of Siebold's theory. He did not venture fully to identify the bladder-worms with the encysted tape-worms, but noted the following distinction between them—"that the former seemed to be pathologically degenerated by the accumulation of a dropsical fluid in the hinder part of the body, and would possibly never be able to become mature tape-worms."

This is, indeed, the opinion which is maintained by v. Siebold in his later work on tape-worms and bladder-worms,[3] and which, supported by the authority of a famous name, has still been held by many even within the last few years.

The morphological identity between the *Cysticerci* and the "second developmental stage" of the Cestodes had been asserted by van Beneden[4] even before Stein. It was, it is true, in connection, not with *Tæniæ*, but with marine tape-worms—the *Tetrarhynchi*—that the former had studied this second stage, but that does not in any way affect the importance of his statement. On the contrary, he thereby further proved that the cystic stage was in nowise confined to the *Tæniæ*, but had a wide, perhaps general, distribution among the Cestodes.

But not only did van Beneden prove the existence of a cysticercoid stage in the *Tetrarhynchi*; he also called attention to this fact, that the cysticercoid *Tetrarhynchus* (*Anthocephalus*) was found especially in the bony fish, and that they afterwards passed over to the rays and sharks, in which the adult *Tetrarhynchus* (*Rhynchobothrius*) was

[1] "Enthelminthica.," Dissert. inaug. Berol., p. 30, 1848.
[2] "Die Cestoden im Allgemeinen," *Prager Vierteljahrsschr.*, *loc. cit.*, p. 9 *et seq.*, 1853.
[3] "Ueber die Band- und Blasenwürmer nebst einer Einleitung über die Entstehung der Eingeweidewürmer," p. 60, 1854.
[4] "Les vers Cestoides," p. 83, 1850.

found. This transference occurred, of course, when the first hosts were eaten by the second. In a great many instances he was even able to follow the metamorphoses step by step, and thus really to prove that in these marine Cestodes the already supposed division of the developmental history into two epochs or stages, spent in different hosts, was an actual fact.

The observations of van Beneden would have made more impression if the illustrious zoologist had been able to trace the development back to the six-hooked embryo. The existence of this embryo was unfortunately but little attended to, and the formation of the cysticercoid forms was connected simply with a stage in which the young worm (*Scolex*, Rud.) had essentially the organization of the subsequently formed head.

And further, van Beneden agreed with v. Siebold in thinking that the cysticercoid stage of the Cestodes was not absolutely necessary but rather accidental, and that it only occurred when the germ was not directly transferred to the alimentary canal.[1] In this way the migrations described by van Beneden lost a large part of their significance. They were characterised more as accidental than as normal processes.[2]

Our knowledge of the development of the Cestodes was thus still far from satisfactory. It was Küchenmeister again who led us in the right direction by a fortunate experiment.

In August 1853 Küchenmeister[3] fed a wether with the ripe proglottides of a tape-worm, which had been reared in the intestine of a dog from the familiar bladder-worm of the sheep (*Cœnurus*). Eighteen days after he found in the brain of the now diseased wether a number of small round bladders, which he identified with young *Cœnuri*, and which were in fact perfectly identical with the bladders which Haubner had described as their first stage.

Thus it was proved that the six-hooked Cestode embryo, if transferred to the alimentary canal of an animal, wanders from the latter, and settling in other organs, often far removed, becomes by metamorphosis a bladder-worm.

[1] "Je crois que le phénomène de l'involvation (*i.e.*, the formation of a cysticercoid *Tetrarhynchus*) ne se montre que chez les Scolex qui arrivent dans les replis péritonéaux, comme aussi les Scolex de Ténia ne deviennent Cysticerques que dans des conditions analogues."—*Loc. cit.*, p. 82.

[2] Afterwards, in his great work on the intestinal worms, which appeared in 1858, and therefore several years after the researches of Küchenmeister, v. Siebold, Wagener, and myself, he abandoned his earlier theory, and correctly explained the life-history and development of the Cestodes. It is, therefore, hardly consistent with historical fact for van Beneden to claim, as he does in a recent work ("Die Schmarotzer des Thierreiches," p. 119, 1876), that he was the first to disclose the true meaning of Cestode development.

[3] *Günsburg's Zeitschr. f. klin. Vorträge*, p. 448, 1853.

This experiment of Küchenmeister did not long remain alone. Even before it was published I had made a similar experiment with the eggs of the tape-worm of the cat (*T. crassicollis*). I fed a number of mice with these eggs, and was able very soon after Küchenmeister to report[1] that five of the six mice experimented on were found to have their livers infested with bladder-worms (*Cysticercus fasciolaris*), while those not fed remained perfectly healthy.

The important results of the experimental method became still more evident when Haubner and Küchenmeister, working with abundant material at the expense of the Government of Saxony, proved that they could, in the above described way, produce the familiar forms of bladder-worm at will and in the greatest abundance.[2] And it was always only the "dropsically degenerated" bladder-worms which grew into mature tape-worms when transferred by feeding to other suitable hosts.

Nor were such experiments confined to Saxony under Küchenmeister's eyes, but had equally successful results in Berlin, Louvain, Copenhagen, Giessen, Vienna, and afterwards also in Toulouse, Alfort, London, &c. Specially convincing was the result of a "feeding" experiment made simultaneously with some of Küchenmeister's material (*Tænia cœnurus*) by van Beneden in Louvain, Eschricht in Copenhagen, and by me in Giessen, in all which the animals under experiment (lambs) became pathologically affected with exactly identical phenomena.[3]

After these abundant and harmonious results, the migrations and metamorphosis of the six-hooked tape-worm embryos could no longer be regarded as abnormal.

But the task of scientific investigation was not yet ended. It was still necessary to follow the gradual development of the bladder-worm from the embryo, and to demonstrate the ways and means by which the latter reached the host, and the organ in which it was to undergo its further development. And in this connection I think I may claim some share in advancing our knowledge of the Cestode development, and that through numerous methodical feeding experiments.[4]

But before I shortly summarise these results, I must glance at the

[1] *Götting. gel. Anzeigen*, No. 66, 1854 (report on Küchenmeister's work on Cestodes); *Gurlt's Mag. f. Thierarzneikunde*, p. 263, 1854.

[2] *Gurlt's Mag.*, p. 243, 1854 (*Cœnurus*), p. 367 (*Cysticercus pisiformis, C. tenuicollis, Cœnurus*), p. 100, 1855 (*C. cellulosæ, Cœnurus*).

[3] *Gurlt's Mag.*, p. 504, 1854.

[4] "Amtlicher Bericht der Göttinger Naturf.-Versammlung," p. 89, 1854; *Ann. Sci. Nat.*, t. iii., p. 351, 1855; "Die Blasenwürmer und ihre Entwickelung," p. 74 *et seq.* 1856.

objection—formerly often urged—that an essentially new factor in the life-history of the animal was introduced by such experiments. In reality, the experiment is only a methodical repetition of natural processes. Just as the animals experimented on were in this case compelled to swallow a tape-worm joint, so they do unconsciously and by chance in the unconstrained course of nature. The proglottides gain the exterior occasionally by spontaneous effort, but usually along with the fæces; they are capable of some motion; they represent, as we have seen, not joints, but independent animals. In warm, damp environment they can retain their motion and life even for days. They leave the filthy surroundings in which they first find themselves, and seek another abode. Like snails they creep along the ground, climbing up a stalk of grass or shrub, and waiting there till eaten by some animal or other. In the dung-eating swine, &c., the transmission is effected directly from the dung. If the new host afford the requisite environment, then the embryos lose their egg-shells and begin their internal wanderings and metamorphoses.

The characteristic and advantage of experiment, as opposed to observation of the natural process, lies in the choice of the host and the control of the amount introduced. I will not indeed assert that the young brood of the tape-worms always reach their host surrounded by their living parent covering. Apart from those cases (Bothriadæ) in which the eggs are liberated and reach the exterior by themselves, the same result might easily follow from the death or rupture of the expelled proglottis. In favourable conditions these isolated eggs remain for long capable of further development. I have been able to infect rabbits with eggs of *Tænia serrata*, which had (in September) been kept twelve days in water, and similarly, Röll in Vienna, has had successful results with proglottides which has lain ten days in the open air, and which had even begun to get covered with mould. It is not yet possible to tell how long this potency can be retained; the period will doubtless vary with the environment. While Gerlach[1] was able to infect a pig with decaying proglottides of *Tænia solium* five weeks old, in an experiment I made, the eggs of *Tænia cœnurus* had lost potency after lying in water for eight weeks.[2] This follows more rapidly when the eggs are kept dry. Haubner reports having ineffectually fed a sheep with tape-worm eggs which had been kept dry for fourteen and for twenty-four days, and I have had similar experience in which eggs exposed to an August sun had lost their power of germinating after four-and-twenty hours.

[1] *Zweiter Jahresber. d. kgl. Thierarzneischule*, p. 66, Hanover, 1869.

[2] Davaine, on the other hand, asserts that he has kept eggs of *Tænia solium* and *Tænia serrata* in water for years, living and unaltered. (*Mém. Soc. biolog.*, t. iii., p. 272, 1862.)

These isolated eggs, then, may also find their way into the intestine of their host along with food and drink, and develop further if they have retained their germinal potency, and if the environment be favourable.

A spontaneous liberation of the embryo does not occur in the *Tæniæ.* There are, however, Cestodes, as we have mentioned, in which this does occur, but these all belong to the species with uterine opening, and with large yolk-containing eggs—that is, to the group of the Bothriadæ.[1] In such cases the embryos (Fig. 177) possess a ciliated coat, by means of which they swim about after liberation. The process of getting free is easy enough since the eggs of these species are provided at one pole with a little lid (Fig. 171), which is lifted up in obedience to pressure from within. In the Tæniadæ there is no such apparatus; the eggs have a completely closed shell (Figs. 173 and 175), and the embryos only become free after the eggs have been transported into the stomach of an animal where the shell is dissolved or softened by the digestive juices.

According to my researches on rabbits fed with eggs and proglottides of the *Tænia serrata* of the dog, this liberation takes place in about four or five hours after the transference, and therefore at a time when the fleshy mass of the proglottides has yielded to the digestive juices. When the resistance is less, the time required will also be less. In the species named, which is probably representative of the other cystic tape-worms, it is not strictly a solution of the shell that liberates the embryo, but rather a rupture, which results from its increasing brittleness and the internal movements of the hooks.

After becoming free, the embryos seem to pass some little time in the stomach. Some at once begin by means of their hooks to bore through the gastric walls to some other organ; others pass directly to the intestine, whence they also bore their way, usually at some distance from the pylorus. It has not indeed been as yet possible to capture the six-hooked embryo in its passage through the intestinal wall, but this is hardly to be expected in the higher and larger animals; nor have other animals been as yet investigated in reference to this point. Yet there can be no doubt as to the fact that the embryos do really perforate the wall of the intestine;[2] they are in their subsequent

[1] The discovery of these ciliated embryos is due to Schubart, who was first able to develop the eggs of *Bothriocephalus latus.* The early death of this promising young investigator hindered the publication of his observations, so that they were first made known at the Bonn Naturalists' Meeting in 1857, through his friend Verloren, who exhibited Schubart's illustrations. The report of Platner, according to which a ciliated coating is also to be observed in the early stage of the embryo of *Tænia solium*, is based on error (*Müller's Archiv f. Anat. u. Physiol.*, p. 278, 1859).

[2] [Raum (Beiträge zur Entwickelungsgesch. d. Cysticercen," p. 28 : Dorpat, 1883)

stages found, according to circumstances, in the most diverse organs, now in the liver or in the lungs, now in the muscles or in the connective tissue, and even in the brain and eye. It is, however, generally the liver which is temporarily or permanently inhabited by cystic worms.

Küchenmeister has tried to explain this special preference for the liver [1] by supposing that the six-hooked brood, after becoming free, seek out the bile-duct, and thus pass directly into the liver, but there is no warrant for this supposition. I have examined perhaps a dozen rabbits in the course of the first day or two after infection, and I never found the embryos in the bile-ducts, though their presence there could have been detected without much difficulty. On the other hand, I have several times succeeded in finding unchanged embryos in the portal vein, and have thus proved that at least some of the wandering embryos get into the venous system, and are carried through their host by the blood-stream.[2] With this agrees Leisering's[3] statement that in the case of a lamb which was fed with *Tænia marginata*, and died five days after with symptoms of icterus, he found "hundreds" of small "point-like" worms in the much enlarged network of the portal vein. These could be nothing but the further development of the young brood, although the embryos of *T. serrata* would, as we shall see, by that time have reached and become encapsuled in the liver. It is therefore natural to connect the frequent occurrence of cystic worms in the liver with their wanderings into the blood-vessels, since the capillary network in the liver is the first at which the embryos would arrive, and since the size of the latter (on an average about 0·022-0·028 mm.) hardly admits of a free passage.

It is, of course, still a moot-point whether this is the only way which the embryos can successfully pursue. This much at least is certain, that there are tape-worms which do not spend their youth in the liver with anything like the same constancy as *Tænia serrata* and *T. marginata*, but are indeed found far more frequently in other organs, such as the muscles or brain. Judging from the mode of dis-

has actually found the embryos of *Tænia crassicollis* in the intestinal wall of the mouse. It was especially the middle portion of the small intestine where the embryos were seen in the free condition, and sometimes in such numbers that ten could be counted in one field of the microscope.—R. L.].

[1] So at least in the first edition of his work on parasites. Afterwards, in the second edition (p. 52), he supposes that the parasites are carried throughout the body by the blood and lymphatic vessels, especially by the latter.

[2] [In agreement with this, Raum (*loc. cit.*, p. 30) has found six-hooked embryos of *Tænia crassicollis* in blood from the portal vein of mice, into which they had been introduced nine, twenty-seven, and fifty-two hours previously; as also in the capillaries of the liver, where their further development could also be studied. The bile-duct was free from embryos.—R. L.]

[3] *Bericht über das Veterinärwesen Sachsens*, p. 22, 1857–58.

tribution which I have established in the case of *Trichina*, one is inclined to suppose that in the above cases the wandering is through the connective tissue substance, and that the embryos bore through the intestinal wall into the body-cavity, in which they wander where they will. I am inclined to support this theory, particularly in the case of the common tape-worm of man, which presents in its occurrence and the distribution of its cystic forms close resemblances to *Trichina*.[1]

When the six-hooked embryos have once reached their future resting-place their further development begins. Originally perceptible only by help of the microscope, they increase so rapidly that they are often in a few days visible to the naked eye. Further, by their pressure on the infected organs, the growing worms cause a proliferation of cells which, completely surrounding the worms, make them look larger than they really are. These cells become in course of time the coating of the cystic bladder, provided no change of position occurs.

In many cases this proliferation of cells is so marked that it has been reckoned as the result of a decidedly inflammatory process. Thus the *Cœnuri*, which wander into the lamb's brain (Fig. 181), surround themselves with a thick, exuded sheath, which becomes drawn out into long bands, in consequence of continued wandering (p. 135). Similarly, in the rabbits infected[2] with *Tænia serrata*, the liver was, on the fourth or fifth day after infection, seen to be studded with white

FIG. 181.—Brain of a lamb with passages of *Cœnurus* (natural size).

points or knots, which were most deceptively like miliary tubercles, but in two or three days after had grown to 0·5 mm., and were, like the *Coccidium*-nodules (p. 207), surrounded by an envelope of connective tissue.[3] The young bladder-worm lying inside is much

[1] Thus, according to Fürstenberg, the embryos of *Tænia cœnurus* reach the brain through the foramina, *via* the connective tissue. (*Ann. d. Landwirthschaft in den kgl. preuss. Staaten*, Jahrg. xxiii., pp. 43 and 166, 1865.)

[2] See "Blasenbandwürmer," p. 121, tab. 1, fig. 1.

[3] I ought to mention here that the growth and development of the bladder-worms are by no means alike in all cases. Not only do the different organs infested induce numerous

smaller, and measures not more than about 0·1 mm. Embryonic hooks cannot, therefore, be demonstrated with any certainty. A histological differentiation now sets in, and is inaugurated by a clearing up of the central portion of the body-mass. This is due to large, clear, non-granular vesicles, which have an almost drop-like appearance, and which grow so rapidly that the inner parenchyma is soon seen as a distinct tissue, different from the cortical layer. In the second week one can distinguish in the worm, which has now grown to 0·5 mm. or more, the first traces of the subsequent musculature through the not inconsiderably thickened cuticle. These are in the form of fine fibres, which run in close groups in two directions at right angles to one another; the outer are the circular, the inner the longitudinal fibres. In appearance and arrangement they resemble the subcuticular musculature of the adult Cestodes (p. 290).

FIG. 182.—A piece of a rabbit's liver with bladder-worm passages (*Cysticercus pisiformis*) (× 10).

One must not suppose that the worms could not move before these muscular fibres were distinguishable; in fact, the form of the body is seen to change, constricting itself here and there, the contractions passing peristaltically up or down. The motions are, indeed, weak and slow, but even the musculature is not able at first greatly to accelerate them.

FIG. 183.—*Cysticercus pisiformis* before the development of the head, with granular sheath and cyst (× 60).

The cortical layer, running under the subcuticular muscles, consists of small, closely pressed nucleated cells, with numerous shining, fat-like molecular bodies often grouped together. Next there are the above-mentioned drop-like vesicles, which have between them a clear, sparsely developed substance, and are considerably larger than in the former stage.

But after a short time the cortical layer undergoes a further differentiation. The cells, of the deeper layer at least, form a clear, tough, connective tissue mass, penetrated by numerous cross muscular

variations, as may be strikingly seen by comparing the young bladder-worms of the brain (*Cysticercus cellulosæ*) with those found in the muscles, but even in the same organ we usually find bladder-worms of diverse size and differentiation.

fibres. Near the cuticle the cells at first retain their original nature; but after the formation of the head they also change, stretching themselves out, and finally becoming for the most part the subcuticular spindle-cells which we have already studied.

As to the arrangement of the muscle fibres, they are most easily understood by reference to later stages. One can distinguish two kinds of fibres—thicker and thinner. The former lie deeper, and are grouped together internally to the cortex as a loose, much interrupted sheath. The fibrils, on the other hand, form a network with cubical meshes, which penetrates the cortex and becomes connected with the processes of the subcuticula. It is, however, doubtful whether these two kinds of fibres form two distinct systems, for the thicker fibres not only split and branch, but are at many places directly continued into the network of fibrils.

While the differentiation of the cortical layer is progressing, the young cystic worm begins to excrete that watery fluid, whose presence has originated the name "bladder-worm," and given occasion to the theory of "dropsical" worms. I am not able to express a decided opinion as to the exact nature of this process, to say whether it results from the flowing together of the interstitial cells, or from the accumulation of the lymph among the parenchyma; yet from my observations of *Cysticercus pisiformis* I am inclined to adopt the former theory. This bladder-worm differs from its allies in this, that it is only at a subsequent stage, when about four weeks old and from 4 to 5 mm. long, that it becomes a true bladder-worm. Till then it is wholly parenchymatous, filled internally with a mucous tissue, with large vesicles, which is hardly at all sharply distinguished from the cortical layer, but is, like it, penetrated in various directions by muscular fibres. In this form I was able to convince myself that the fluid first collected in vacuole-like spaces, which became ever more distended, and finally flowed together. The interstitial tissue was, of course, thereby destroyed, so that one could often observe how the muscular fibres projected more or less into the water-filled space, either freely or with attached shreds.

An indirect proof of the correctness of this theory is also, I think, to be found in the fact that in the ordinary *Cysticerci*, where the excretion takes place very early (in some when they hardly measure 0·3 mm.), and is much more copious than in *Cysticercus pisiformis*, the bladder-like body consists solely of the above-described cortical layer. The accumulation of fluid has therefore gone on at the expense of the former internal substance. A specially formed border sheath is in such cases wanting, the inner surface of the subcuticular connective substance being itself directly washed by the fluid.

The state of matters in *Cysticercus pisiformis* further shows us that the excretion and accumulation of fluid in the interior of the bladder-worms do not by any means always occur in the same complete fashion. I have lately come to know of a number of *Cysticerci* which had, strictly speaking, no bladder, since the accumulation of water had either never occurred, or only to an extremely small extent. They were all tape-worms without hooks, but I was unfortunately unable to identify them. One of these forms is probably identical with Diesing's *Piestocystis variabilis* (Fig. 184). I observed it in the lungs of the crow—only once indeed, but in tolerable abundance.

Fig. 184. — Longitudinal section of an unarmed cystic worm from the lung of the crow (*Piestocystis variabilis*, Diesing ?) (× 30.)

Fig. 185.—Unarmed cystic worm from the body-cavity of *Lacerta vivipara* (*Piestocystis Dithyridium*, Diesing). *A*, with head invaginated; *B*, with head half extruded; *C*, with evaginated head. (× 30.)

The bladder has an extremely thick wall, and is filled internally with a mucous tissue which surrounds the narrow bladder-cavity on all sides. Two other allied forms—one from the sub-epidermal tissue of the nightingale, and another (Fig. 185) from the body-cavity of *Lacerta vivipara* (*Piestocystis Dithyridium*, Diesing) — are wholly destitute of a bladder-cavity. The interior of the body consists of an interlaced connective substance, which is only so far variable in that its consistency decreases towards the centre. With the loss of the bladder-cavity, most of the characteristic peculiarities of the bladder-worms have been also lost, so that it is hardly possible to distinguish these forms from developed bladder-worms with evaginated heads. In fact, even in spite of the attached caudal bladder, such a form as that represented on Fig. 185, *C*, looks exactly like a young, still unsegmented tape-worm.

Almost contemporaneously with the differentiation of the cortical cells, a new formation occurs in the peripheral tissue. In some way not clearly understood, there arises in that region what we have already discussed in the adult tape-worm as the excretory system.[1] Here and there one observes a clear, usually stellate, finely branched streak, in which one can afterwards detect the parts of a vascular network which surrounds the whole bladder, and rapidly attains a considerable development. But before the formation of the head, it is not possible to distinguish longitudinal and transverse vessels ; it is simply a network with meshes of varying size and diverse arrangement. From the larger stems, there spring numerous fine branches ramifying like a tree, which apply themselves to the surface of the bladder, and pass between the fibrils into a second finer network (see Fig. 199). No communication with the watery internal space is observable. On the other hand, we can recognise in the peripheral vessels the same ciliated apparatus which we noted in the vascular system of the adult Cestodes. They are exceedingly numerous in *Cysticercus pisiformis*, and are in continual undulating motion. I have not been able to decide whether the cilia are seated on the ordinary walls of the vessels, or on special funnels appended to the vessels, and in connection with cavities in the connective substance.[2] The latter is supposed to be true in the case of young Distomes. At any rate this apparatus in the bladder must have the same significance as in the adult Cestodes. The resemblance becomes still more complete when we learn from Wagener that the vascular system even in the bladder-worm communicates with the exterior by means of a short contractile tube at the posterior pole.

I have been able to convince myself of the existence of this terminal funnel only in the above-mentioned hookless *Cysticercus* from *Lacerta vivipara* (Fig. 185). It is clad with a thickish cuticle, probably resulting from an invagination, and leads to two (or four ?) vessels which ascend to the head at some distance from the surface, and give off in their course numerous lateral branches.

The young bladder-worm persists for a while as a simple more or less spherical watery bladder, until the formation of the subsequent tape-worm head inaugurates a new epoch. In *Echinococcus* this takes place only after several months, when the bladder has grown to perhaps the size of a nut ; in the *Cœnurus* it occurs in the fifth week, when the worm is as large as a pea ; in the *Cysticercus* proper it

[1] In my monographs on cystic worms, I erroneously referred the appearance of this vascular system in *Cysticercus pisiformis* to a later developmental stage.

[2] Bütschli, "Bemerkungen über den excretorischen Gefässapparat der Trematoden," *Zool. Anzeiger*, Jahrg. ii, p. 588, 1879 ; see also the first German edition of this work, Bd. i., p. 766.

appears still earlier, usually in the course of the third week, when the bladder is hardly 1 mm. in size, if so much. Only the bladder-worm of the rabbit attains at this time to a length of more than 2 mm. (cross diameter = 0·4 mm.), having at an early stage changed from a globular to an extended form.

The first trace of the head is seen in the subcuticular layer of cells—the most important layer in the formative history of these organisms. At a distinct point which we may call the anterior pole, and which is easily recognisable as such in extended forms like *Cysticercus pisiformis*, an active vegetative process sets in. In consequence of this, the cellular layer becomes thickened into a meniscus, which soon forms a little protuberance, and grows ever further inwards into the bladder-cavity or the substance which fills it.

As soon as this has gone on for some little time, a pit-like depression arises on the outer covering of the body, which increases in depth as the protuberance grows, and finally broadens out at its lower portion into a bottle-shaped cavity. The rudiment of the head is thus not solid, but hollow, and its cavity is to be regarded as an invagination from without, especially since the cuticle of the bladder is continued inwards through the outer opening, and completely lines the interior.

Fig. 186.—Young bladder-worms of *Tænia saginata*. (× 30.)

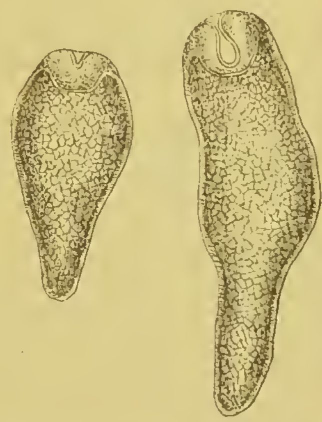


Fig. 187.—Young bladder-worms of *T. serrata*, with rudiment of head. (× 12.)

During the deepening process, the lining envelope is sometimes changed. I have seen bladder-worms in which two or three discharged cuticular membranes lay like conical shells one within the other. At this stage, too, one can directly observe the new formation of the cuticle over the bladder, and this much more distinctly than afterwards, since in these young forms the old skin is usually discharged as a continuous sheath, and remains lying for a while near the body. It is loose and thick, and therefore quite different from the thin new cuticle lying below.

The substance of the newly formed head consists of the same small nucleated cells which we found in the subcuticular sheath, whence, indeed, it originated. As soon as it begins to raise itself more prominently, and to grow out like a clapper, one can see on the surface turned towards the bladder-cavity a thick envelope of a fibrous character. The head of the bladder-worm is, in other words, enclosed in a sac which separates it from the rest of the body, and which can still be recognised as a special formation when the enclosed cells have completed their metamorphosis. I have proposed for this envelope the name "receptacle"[1] (*receptaculum scolecis*), and am still inclined to support this proposal, although I have meanwhile come to hold a

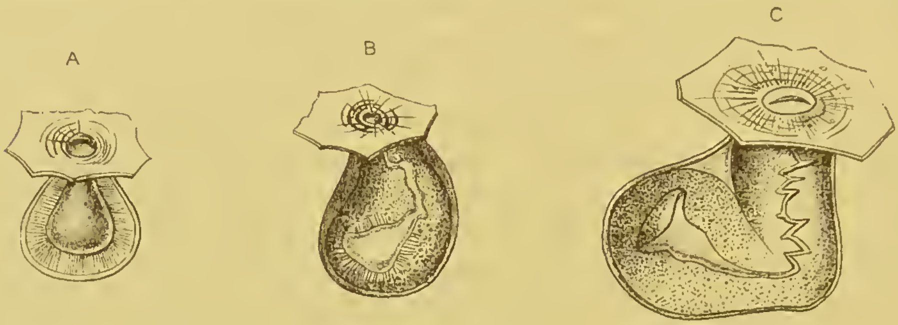


FIG. 188.—Various stages in the formation of the head of *Cysticercus cellulosæ*, showing the receptacle. (× 45.)

different opinion as to the nature of the organ in question. I was formerly of opinion that this receptacle originated from a differentiation of the cellular mass of the head, and was indeed genetically a part of the head, but I have subsequently become convinced that it belongs to the inner layer of muscular fibres which run inside the bladder, and which are pushed into a sac by the elevation of the head, the cells of which have a more peripheral position. Of course, one must not suppose from this statement that the receptacle is simply formed by a distention of the inner layer of muscles, and that it only contains the muscular fibres which formerly overlaid the cellular rudiment of the head. On the contrary, there can be no doubt that new elements become associated with these old muscular fibres during the

[1] Von Siebold has also used this term in his work on tape-worms and bladder-worms, but in quite another sense, namely to denote the proper body of the bladder-worm (the enlarged six-hooked embryo). Küchenmeister also speaks of a receptacle in the new edition of his work on Parasites (p. 61), but understands by the term the primitive rudiment of the head, which he does not recognise as such, but regards as a brood capsule, which subsequently bears the tape-worm head. Indeed the description he gives of the development of the bladder-worm is such a strange mixture of capricious imagination and confused representation, that I must decline entering into its details.

elevation and growth of the head, or, in other words, that the receptacle is formed by further differentiation of the muscular layer of the bladder, just as the head proper is formed from the subcuticular sheath. Nor can the receptacle and head be distinguished so sharply from one another as is at first apparently the case. As the muscular sheath and the cellular layer are bound together in the wall of the bladder, so we can always demonstrate a connection between the receptacle and its contents (Fig. 197), a connection which extends over the whole surface, or is in some species confined to certain points.

Thus the receptacle is not in every case an equally independent structure. It has least independence in the bladder-worms with parenchymatous bodies, such as we have seen in *Cysticercus* (*Piestocystis*) *variabilis* and its allies, for there it is not only connected with the mass of the head, but is, like the ordinary body muscles, bound up with the tissue of the bladder. One can observe how the muscular sheath which runs between the cortex and the inner parenchyma (Fig. 197) bends backwards at the anterior end, and surrounds the head as a sac, and how the individual fibres often separate themselves from the receptacle, and mingle with the parenchyma. The state of matters is very similar in *Cysticercus pisiformis* where the bladder-worm body preserves anteriorly its original parenchymatous character, so that the receptacle is united on all sides to a loose connective substance. The only difference which can be observed is that the fibres of the receptacle are more closely appressed and more firmly interwoven.

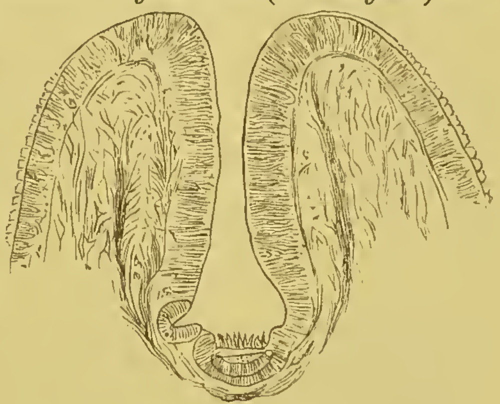


Fig. 189.—Cephalic end of a young bladder-worm from the rabbit, showing the still imperfectly developed hooks. (× 45.)

Where the inner parenchyma is wholly obliterated by the accumulating water, as in the majority of true bladder-worms, the receptacle of course acquires a distinct external boundary. The connection with the body of the bladder becomes in such cases restricted to the basal portion of the head, where one can observe the fibres passing directly into the muscular sheath.

As a rule, however, it is only the exterior surface of the receptacle which attains this independence ; for the inner surface remains usually in general, though, as we shall afterwards see (Fig. 197), in loose connection with the head. The bladder-worm of *Tænia solium*, the

so-called *Cysticercus cellulosæ*, is almost the only instance of another state of affairs. There the receptacle is separate from the head, and becomes a sac-like envelope, wholly free except at a restricted region posteriorly. This peculiarity is connected with the fact that the head of this bladder-worm, instead of growing in proportion to the receptacle, as is usually the case for a lengthened period, becomes rapidly and considerably elongated, and is at an early stage bent like a knee inside the sac (Fig. 188, *C*).

The head remains in this state till it acquires a length of perhaps a millimetre. This growth is accompanied only by histological changes. These are most striking in the neighbourhood of the cuticle which clothes the interior of the head, and which afterwards becomes the cuticular covering of the head of the tape-worm. Here, at a position which corresponds to the subcuticular sheath, the hitherto indifferent cellular mass assumes very early a radiate structure (Fig. 188, *A*). This is brought about by the cells growing out into a layer of closely appressed radiate fibres. These are the structures which we described in the tape-worm (p. 288) as subcuticular fibre-cells. At first sight one might regard them as epithelial cylindrical cells. Indeed they seem to have the epithelial structure of the subcuticula; but this appearance is quite deceptive. The close grouping, which makes them look like a cellular layer, is caused by the absence of an interstitial connective tissue. When this is subsequently developed, one can recognise the truth of our position, and that more clearly in the bladder-worm than in the adult form. To be undeniably convinced of the true nature of the subcuticula, it is sufficient to make a thin section of the swollen pad of connective tissue on the head of a *Cœnurus*, or on the bladder of *Cysticercus pisiformis*, which is further penetrated by an extraordinary number of distinct cross fibres.

As soon as the subcuticula acquires this radiate structure the adjacent cells of the head begin their histological metamorphosis. For the most part at least they become extended, and grow into fibres, which, in spite of the still distinct nucleus, are undeniably muscular fibres. The course and direction of the fibres are at first indistinct, gradually, however, they become better defined, those next the subcuticula assuming a longitudinal direction, those further outwards becoming rather transverse. Of course this applies only to the main bands, for there are many deviations in detail.

At this time the rudiments of the vascular system appear. One can recognise four longitudinal stems which spring at the insertion of the head from the vascular system of the bladder, run downwards to the outside of the longitudinal fibres, and become at the wider end

united by a circular vessel into a connected system. Afterwards one can observe the formation of a number of fine twigs, with ramifying processes and ciliated organs.

FIG. 190.—Head of *Cysticercus pisiformis*, with vascular system. (× 45.)

At the same time the first calcareous bodies make their appearance, and that primarily and principally at the point from which the head springs, whence they spread in ever-increasing numbers. Occasionally a few of these concretions are to be found even before this round about the head. The body of the bladder is, as a rule, but sparsely supplied with them, though there are exceptions, such as *Piestocystis*.

In order to understand the further development of the head in the tape-worms, one must imagine it as a cylindrical structure, not solid, as it appears, but with a blind cavity running up its whole length. If we suppose this head to pass posteriorly, not into the jointed body of the adult tape-worm, but into a hollow bladder, into which it is indeed invaginated, then we have a representation of the primitive state of head in the bladder-worms we are discussing (Fig. 191). The surface of the rudimentary head next the receptacle represents the subsequent inner parenchyma, while the future outer surface, with the cuticle, lines the cavity of the clapper-like rudiment. The tape-worm head thus originates within the bladder, as Göze, and Wagener after him, observed, and occupies an "inverted position."

FIG. 191.—Head of *Cysticercus pisiformis* just mature. (× 40.)

One is most distinctly convinced of this arrangement by noting the formation of the suckers and hooks which generally appear soon after the first rudiments of the head are formed. They are first seen at the distended lower end of the bottle-shaped cavity, the circle of hooks lowermost, the suckers somewhat higher where the cavity is widest.[1] Their relative position is therefore the reverse of the final one, where the hooks are on the apex above the suckers.

[1] With this agree the results of van Beneden on the development of *Cysticercus pisiformis*, as detailed in his "Vers intestinaux," p. 238, 1858. Moniez, however, describes an entirely different mode of formation. I shall afterwards return to the discussion of his theory, but will only here remark that I have repeatedly and most distinctly convinced myself of the truth of my statements.

Thus we understand how it is that, in transverse seetions of the lower part of the rudimentary head (Fig. 192), we come upon some where the four suckers are seen all opening into the eentral space. Such a section must of eourse be above the hooks. I ought also to mention that one frequently finds cases where the apieal surface is pushed outwards,[1] so that the hooks (Fig. 193) come to be about the same level as the suckers. I believe that this occurs espeeially in specimens which have been suddenly killed by spirit, &c., while in full possession of their powers of eontraetion.[2] Although this pushing outwards occasionally oeeurs early, even before the formation of the hooks (Fig. 188, *C*), I think it is to be regarded as the result only of a secondary alteration, probably determined by a eontraetion of the surrounding museulature.

FIG. 192. — Transverse section of the anterior end of the bladder-worm of the rabbit, at the level of the suckers. (× 40.)

FIG. 193.—Longitudinal section through the head of a bladder-worm from the rabbit, where the crown of the head is pushed outwards. (× 60.)

Before passing to describe the metamorphoses of the head, I may remind the reader that the eavity is widened out at the lower end, whieh, as the embryo grows in length, beeomes ever more sharply

[1] The original here has "inwards" (nach Innen), referring to the cavity of the invaginated head. I think it better to use the word "outwards," meaning "towards the periphery of the bladder."—W. E. H.

[2] I infer this from the fact that in my earlier investigations, which were mostly on living specimens, this appearance but rarely occurred, while I observed it frequently when working with hardened specimens.

distinguished from the other more canal-like portion. It is this lower enlargement which is the seat of all those processes which give the head its characteristic form, and which are at this time (in *Cysticercus pisiformis* in the course of the fourth week) progressing, so far at least as suckers, hooks, and rostellum are concerned.

The formation of the suckers is most striking. It is introduced by a change in the form of the inner space, which is produced inwards to form little pockets in the substance of the head-walls; these occur at four points, at equal distances from one another. They become more and more markedly distinct from the rest of the internal space, and represent, of course, the cavities of the suckers. The musculature, which forms such an important part of the apparatus, then arises (Fig. 195); the subcuticular sheath, with its radiately arranged cells, surrounds each pocket like a hood, and becomes an independent structure, in which the characteristic arrangement of the muscular fibres very soon appears. The fact that the radiate fibres, which form the greater part of the musculature, arise from the subcuticular cells, seems to be in favour of the opinion which we have more than once expressed, that the latter have a closer connection with the muscular than with the epidermal tissue.

The rostellum originates in a closely analogous fashion. The subcuticular tissue at the bottom of the head-cavity (*i.e.*, in the depression between the suckers) which is, as we have seen, occasionally pushed forward into a sort of boss (Fig. 196) forms a cushion (Fig. 194), which is supplied with muscles by the development of the above-mentioned extended cells.

FIG. 194. FIG. 195. FIG. 196.

Metamorphoses of the head of *Cysticercus pisiformis*. (× 45.)

The hooks arise round about the rostellum, or rather on a small circular ridge[1] which surrounds it (Figs. 194, 195). While the hooks

[1] Later observations force me to modify in some particulars the account I previously gave of the history of the circular ridge (first German edition of this work, Bd. i., p. 245).

are gradually becoming mature (for it is only in the hookless *Tænia saginata* that the original state persists), this ridge grows further and further over the rostellum, until (Fig. 189) its margins coalesce in the centre, and form the layer in which the posterior[1] processes of the hooks are embedded (see Fig. 151). The metamorphosis of the hooks themselves has been already described (p. 287). They appear first as soft, thin, little cones, which grow into the cavity of the head with their points upwards and their concave sides turned outwards. Before they become elevated, one finds countless fine points on the periphery of the subsequent rostellum, some of which grow directly into the cones, while the greater number of them speedily disappear.

FIG. 197.—Head and body of *Cœnurus, in situ.* (× 100.)

FIG. 198.—*Cysticercus pisiformis* with head half evaginated. (× 6.)

FIG. 199.—Head and body of *Cysticercus pisiformis* in completely evaginated state. (× 19.)

The histological differentiation is in the majority of cases complete towards the end of the second month. The head has then essentially its adult organisation,[2] and almost its adult size, although it still

[1] The "posterior process of the hook" is the one directed towards the apex of the head.—W. E. H.

[2] I may briefly note that one can already recognise under the rostellum the "plate-like" muscles described by Nitsche (*Zeitschr. f. wiss. Zool.*, Bd. xxiii., p. 181, 1880), and in successful sections the head ganglia. The latter are widely separated from one another by the pressure which acts longitudinally on the head, so that they have the greater part of the rostellum lying between them.

remains inverted in the maternal bladder (Fig. 191). But the development of the bladder-worm is not yet quite complete. The head, which was at first only a little distant from the bladder-wall, becomes ever further removed by the elongation of its basal portion; thus there arises in course of time a distinct verniform body, extending in cylindrical form between the upper narrow neck-like portion of the head and the bladder. Both head and body lie still within the receptacle (Fig. 197). The succession of layers corresponds with that of the head; the surface covered with cuticle is inwards, next the cavity. The musculature is more strongly developed than in the head, and the number of calcareous bodies is usually very considerable.

The older the bladder-worm, the more this body grows; it acquires numerous cross wrinkles and folds, which usually extend far into the canal-like space, and it squeezes itself together in the extended receptacle as far as the space will permit. As a rule, the head takes up a lateral position—which we have already noted in the bladder-worm of the pig—as a natural consequence of the growth in length and early bending of the head (p. 346). The connection with the receptacle presents no special difficulty in the way of this change of position, for the connective substance which has been produced is soft and extensible, and permits many alterations (Fig. 197). If the receptacle be unable completely to contain the contents, then the end of the body which is next the bladder is extruded (Fig. 198) from the opening of the head-cavity, so that the former inner surface comes to be external. Sometimes the whole of the body and head are thus evaginated, so that the bladder-worm becomes (Fig. 199), indeed, like a tape-worm with an incompletely jointed body and an attached "caudal bladder" (*Tœnia visceralis*).

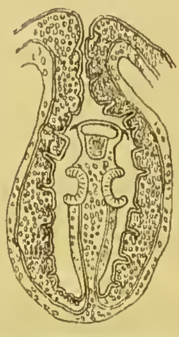
In this evagination the musculature of the bladder has probably a share as well as that of the receptacle. The pressure which the former can exercise affects primarily only the enclosed fluid, but this is transmitted in all directions, and is finally most influential where the resistance is least—namely, at the position of the evaginating head. The process is essentially the same as we formerly (p. 311) described in the protrusion of the penis from the so-called "cirrhus-pouch," which stands to the cirrhus in much the same relation, even anatomically, as the receptacle to its contents. The retraction of the protruded structure can of course be effected only by special muscles.

Though the whole head-mass of the cystic worm has been evaginated, this does not prevent some of the individual parts remaining introverted. This is particularly true of the head proper, which protrudes (Fig. 193) from the bottom of the appendage, and not unfrequently

pushes itself forwards even into the cylindrical body. In this way the cuticular coat comes to lie externally, and the suckers are found under the hooks. When this elevation is complete, as in Fig. 201,[1] then the head is in position and character like the subsequent tapeworm head, and that the more since the inner surfaces, formerly external, soon come into close contact, and form an apparently solid mass.

FIG. 200.

FIG. 201.



FIGS. 200 and 201.—Rudimentary heads of *Tænia serrata* at the beginning (Fig. 200) and at the end (Fig. 201) of the protrusion of the head. (× 20.)

Such appearances have often given rise to the supposition that the bladder-worm had this position and form from the very first. According to this theory, what we have above described as the rudimentary head, and have followed in its metamorphosis step by step, is only a sheath, from the base of which the head subsequently arises as a solid projection.

Moniez, the last author who has discussed the *Cysticerci*, believes he has convinced himself of the truth of this by sections, and explains my opposing, and as he thinks erroneous, results by referring them to my imperfect methods of investigation. It is, of course, true that I first reached these results from the examination of squeezed preparations (1856), but I did not neglect to corroborate them by means of sections when our methods became more perfect. These later observations lead me still to persist in upholding the accuracy of the above outlines, in spite of Moniez's opposition. Moniez has obviously confined his observations mainly to old bladder-worms (*Cysticercus pisiformis*), whose heads have often, as we have noted, lost their original position, and are therefore unfitted to lead one to a true understanding of the mode of origin. The young forms of which he made sections were, as I could see from his preparations, at a stage when the head and its cavity had still but a somewhat undifferentiated formation.

What Moniez considers as the beginning of the head is only a boss-like swelling of the base, such as (see Fig. 196) one not unfrequently finds in violently killed bladder-worms. Far from representing the whole head, this projection is, as we have seen, neither more nor less than its apex with the lenticular rostellum, which, when there is no protrusion, is seen in the form of a meniscus (Fig. 194), with incurved anterior surface. If Moniez had investigated the proper stages, he would have been convinced that the suckers, instead of being

[1] The figure is copied from a preparation kindly lent to me by M. Moniez.

formed at the base of the protrusion, arise above it on the side walls of the bottle-shaped enlargement, and at first appear as pocket-like invaginations, which afterwards become clad with the above-described muscular wall. He would, in other words, have been convinced that it is the primitive head rudiment which is changed into the tape-worm head — at first necessarily invaginated.[1] Besides, even the adult bladders often show in the position of the head traces of the original state, so that one is in no way warranted in regarding the protrusion as a normal or necessary developmental stage.

This is true, indeed, only of the majority of cystic worms, but specially of those in which we are now interested. There are, however, exceptions, as for instance the familiar bladder-worm of the mouse (*Cysticercus fasciolaris*), which becomes *Tænia crassicollis* in the intestine of the cat. In this animal the cylindrical body, which is in other cases hardly ever more than a few millimetres long, gradually grows to a length of several centimetres. The receptacle is unable to contain so large a body, and thus the latter comes to be evaginated along with the head at quite an early stage. In this condition it persists, and is so like an ordinary tape-worm that its cystic nature escaped detection for a long time. In spite of this resemblance, the jointed body of this bladder-worm does not pass into the subsequent tape-worm body any more than any other bladder-worm body does.[2]

FIG. 202.—*Cysticercus fasciolaris* (nat. size).

Mature bladder-worms differ greatly in size and form, as we shall afterwards see. Here we shall only mention that among common forms the smallest is *Cysticercus fasciolaris*, and *C. tenuicollis* (the bladder-worm of *Tænia marginata*) the largest. In the former the bladder is usually not so large as a pea, while in the case of the latter it grows occasionally to half a foot in length or more.

[1] My supposition is corroborated by Moniez's own statement ("Essai monographique sur les Cysticerques," *Travaux de l'Institut. zoolog. de Lille*, t. iii., p. 41 : Paris, 1880), that he has only imperfectly followed the metamorphosis of the head. He seems to have missed just the decisive stages. None the less did he hesitate at once to condemn my results. According to him, what we have called the head-rudiment is only the cradle of the future head. It is a part of the bladder, arising by invagination, and forming the receptacle ; for what I have described as the receptacle is no special organ, but only an outer muscular layer. I must, however, refrain from entering into a discussion of Moniez's statements, and only remark that I cannot concur with the histological results any more than with the developmental.

[2] In the first German edition of this work I held the contrary opinion, which was based on error, as I have long since pointed out in the case of *Cysticercus fasciolaris* (*Zeitschr. f. wiss. Zool.*, Suppl.-Bd. xxx., p. 605, note, 1878).

In the great majority of species the productive power of the bladder is exhausted in the formation of a single tape-worm head, as in the bladder-worms proper, which were referred to the genus *Cysticercus* by the older Helminthologists. The cause of a multiplication of heads is unknown; therefore, we can hardly say that it is not possible for a *Cysticercus* to have at a time two or three heads, instead of only one, and isolated instances of polycephalous bladder-worms have indeed been chronicled,[1] though my observations on *Cysticercus longicollis* of the shrew (*Hypudæus*), (the young stage of *Tænia crassiceps* of the fox), to which most of these reports refer, have caused me to regard these alleged instances with some suspicion.[2] The lappet-like appendages of the caudal bladder, which have been regarded as new heads, turned out to be simple diverticula of the bladder, that is to say, they owed their origin to an irregular growth, determined perhaps by pressure or traction. It seems to be very likely that these structures have a mechanical cause,[3] since I once saw in *Cysticercus pisiformis* a similar diverticulum firmly connected with the enveloping connective tissue capsule, and since the bladder-worms of the common *Tænia* of man often grow out into irregular tubes in the subarachnoidal spaces of the brain, which, with their adherent bladders, sometimes have a quite racemose character, but yet never form new heads.

This polycephalous condition, at most an exception in the *Cysticerci*, occurs constantly in the "stagger-worm" of the sheep; that is, in the cystic stage of the *Tænia cœnurus* of the dog. In this bladder-worm, which is found in the cavities of the skull, a group of three or four heads is present from the first, and the number is continually increased up to several hundreds. The new heads are budded out beside and between the older, and are not irregularly scattered over the whole surface of the bladder, but occur in groups, and only in one (anterior ?) segment of the vesicular body.

FIG. 203.—Heads of *Cœnurus*. (× 25.)

The *Cœnurus* (*Tænia multiplex* of Göze) is related to the *Cysticercus* as a compound to a simple animal—a sufficient reason for systematic zoologists to separate them. But apart from the multiplication of these heads, the structure is the same. Each of these many heads arises just as the single one did (Fig. 197); in origin and structure they are quite analogous. Nor can we regard it as a special characteristic of the *Cœnurus* that the

[1] Especially by Bendz in *Oken's Isis*, p. 814, 1844.

[2] V. Siebold comes to a similar decision, *Zeitschr. f. wiss. Zool.*, Bd. ii., p. 226, 1850.

[3] The "double monster" of *Cysticercus longicollis*, figured by Bremser in his "Icones Helminthum" (Tab. xvii., Fig. 14), is probably to be regarded as due to the above cause.

bladder has often an irregular, more or less diverticular form. This is particularly well seen in those worms which are found outside the cranial cavity, and which are partly perhaps separate species. Sometimes their regular sinuses present an almost racemose appearance, like the the so-called *Cysticercus racemosus.*[1]

In the case of the familiar *Echinococcus,* which originates from the *Tænia echinococcus* living in the intestine of the dog, the state of affairs is somewhat different. We shall afterwards have an opportunity of studying these wonderful structures more closely, and will only now summarise what is necessary in order to understand their relation to other bladder-worms.

Echinococcus is, like *Cœnurus,* polycephalous, but its heads differ not only in their minute size and myriad numbers, but also in their relations to the body of the bladder. For, instead of springing directly from it, as has been hitherto the case, they originate on the wall of special brood-capsules which lie in numbers on the inner wall of the bladder.

Fig. 204.—Brood-capsule of *Echinococcus,* with adherent heads in various stages of development. (× 36.)

Fig. 205.—Diagrammatic representation of a proliferating *Echinococcus.*

The size of these brood-capsules never exceeds 1·5 to 2 mm. in diameter, and even this size is attained only by the oldest capsules, which enclose a dozen or more heads. At first the capsule contains only a single head, but the number gradually increases, new heads being continually budded off from the walls. The process of formation closely resembles that of the head of *Cysticercus.* A diverticulum of the outer surface occurs, which grows out into a hollow cæcum, forming the tape-worm head, as in the ordinary bladder-worm. The completed head then draws itself back into the cavity of the brood-capsule, so that the suckers and hooks become ensheathed by the former neck, and the originally club-shaped appendage now lies like a berry on the inner wall of the capsule. Sometimes this invagination

[1] A striking instance of this has been lately described and figured by Mégnin, *Journ. Anat. et Physiol.*, Pl. vii., 1880. See also Bendz, "Om Oprindelsen af Dreiesygen hos Faaret," *Tidsskrift for Landockonomie*, July 1857, a memoir which has remained to all appearance unnoticed.

occurs at an earlier stage, even before the formation of the head has begun, and then it is complete up to the blind end of the cæcum. The metamorphosis of the head must in such cases of course take place inside the bladder, from which even the perfectly formed heads may be seen for a while projecting, with the hooks and suckers directly outwards. When these are subsequently drawn back to the cervical region, the heads, which have originated in this way, look like the others.

If we suppose that the brood-capsules represent a pushing in of the *Echinococcus*-wall, as is diagrammatically represented in Fig. 205, then the difference between the *Echinococci* and the ordinary bladder-worms, and particularly the *Cœnurus*, is essentially limited to this point, that the heads are budded off from these invaginations, instead of from the proper bladder-wall. This supposition does not as a matter of fact seem so incorrect or unreasonable, although the brood-capsules arise, as we shall afterwards see, without any participation on the part of the cuticle. At any rate we can thus very simply express the essential peculiarities of the *Echinococci*, and their relation to the other bladder-worms.

As to the fact that the cuticle takes no part in the formation of the brood-capsule, this may perhaps find some explanation in the very unusual thickness which we found it to possess in the *Echinococci*. There are some whose cuticle is a millimetre thick, and, besides such instances which occur in the larger forms, even the smaller *Echinococci* are provided with a very thick cuticle; and not only is it very thick, but it also shows a characteristic lamination, which particularly demands our attention, since it not unfrequently happens that new *Echinococcus*-bladders are found between the layers, whence they burst forth either outwards or inwards, often at an early stage, and become independent bladders.[1]

According to the precise nature of this proliferation, various forms of *Echinococcus* have been distinguished, as we shall afterwards see, when we come to discuss in detail this interesting bladder-worm.

As a rule, daughter-bladders and brood-capsules are only formed at a later stage, when the bladder proper has attained a considerable size. Sometimes they seem never to occur. We know at least of numerous cases in which the *Echinococci* produce no daughter-bladders, in which we look in vain for brood-capsules or heads, and yet we are not warranted in distinguishing these—though it has been done—as distinct species.

[1] I may take this opportunity of mentioning that I have to thank Dr. A. Schmid, in Frankfort on the Main, for a *Cysticercus tenuicollis*, whose bladder encloses a few isolated daughter-bladders.

Where the bladder-worm lies in parenchymatous organs rich in connective tissue, it never leaves its cuticle exposed. It is constantly found enclosed in a connective-tissue envelope, which belongs not of course to the worm, but to the host and the organ inhabited. The inner surface of the capsule is smooth, like a serous membrane, and is furnished with a cellular layer, which is possibly of importance in the excretion of the nutritive fluid. We cannot, however, regard the cyst as essential to the nourishment of the animal, since it is wanting in many situations—*e.g.*, in the eye and in the brain. The surface of the *Cœnurus*-cavity (in the brain of the sheep afflicted with staggers) is covered with a tough layer, which is sometimes separable in large shreds, but does not exhibit in any way the ordinary structure of the bladder-worm cyst. One can indeed see in it the remains of nervous substance and vessels in all stages of disintegration and degeneration, —a striking proof of the disastrous effect of parasites.

The connective-tissue cyst of the adult bladder-worm is by no means always identical with that which surrounds the young parasites after their immigration. It only persists when the worm remains in its first resting-place. But occasionally the worm retains for some time the power of changing its abode, especially if the organ in which it has landed is poor in connective substance. In spite of their increased size, the young immigrants press slowly forwards, probably by continuous peristalsis, and press the surrounding tissue to the side. Thus one finds young *Cœnuri* on the surface of the brain, forming passages an inch long, lined with long shreds of exuded matter. Similarly

FIG. 206.—Brain of a lamb with passages of *Cœnurus* (natural size).

the *Cysticerci* of the liver and lungs press ever outwards, and often break through into the body-cavity. There are even species which reach the body-cavity in this way only. To these belongs, for instance, the *Cysticercus pisiformis*, so common in our hares and rabbits. Three or four weeks after an infection with *Tænia serrata*, the liver of these animals is seen to be perforated often by countless white streaks — the borings of the young *Cysticerci* — which almost all gradually lead to the surface, and allow their inmates to get out.

The worms then remain for a while free in the body-cavity, but after some weeks one finds them once more in a cyst hanging usually to the omentum or the connective-tissue covering of the intestines. The *Cysticercus tenuicollis* of our ruminants behaves in an exactly similar way, as we shall afterwards notice in greater detail.

FIG. 207.—A piece of rabbit's liver with passages of *Cysticercus pisiformis*. (× 10.)

According to the observations on which we rely, the development of the cystic worms always begins with the formation of the subsequent bladder. As to the origin of the latter, we have no direct results, but we can hardly be mistaken in regarding it as the enlarged and modified embryonic body.[1] This supposition becomes a certainty when we examine the more microscopic so-called "Cysticercoids," which resemble the above-described bladder-worms in all essentials, and differ only in their minuteness and in the absence of fluid. These parasites are found exclusively in cold-blooded animals, especially among invertebrates, such as insects and molluscs. As yet but few forms are known—not more than a dozen—although we have reason to believe that they far exceed the bladder-worms proper in the number of their species.

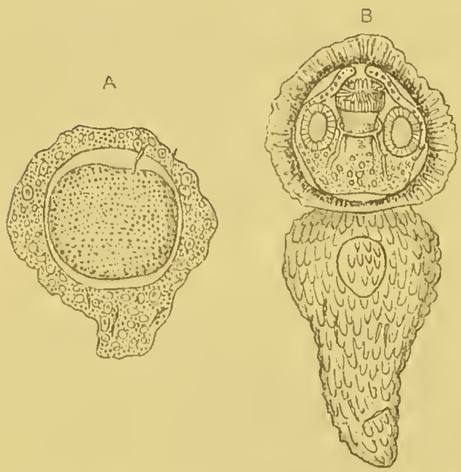


FIG. 208.—Development of *Cysticercus tenebrionis* (after Stein). *A*, Embryo after the hooks are cast off ; *B*, Adult *Cysticercus*. (× about 100.)

In one of these forms, to which we have already (p. 331) referred — the *Cysticercus tenebrionis*, which is probably the young stage of a *Tænia* inhabiting the mouse—Stein has described the gradual passage of the embryonic body into the subsequent bladder. The six-hooked embryo

[1] I believe that I once found the six embryonic hooklets near the anterior end of the body of a young *Cysticercus pisiformis* ("Blasenbandwürmer," p. 120). Professor Ed. van Beneden has, he tells me, been more fortunate, having repeatedly demonstrated these hooks on bladder-worms of *Tænia saginata* 0·4 to 0·5 mm. in size. Three times all the six hooks were present in varying position, while in other cases we could see only a few, or only one. [Raum also (*loc. cit. supra*) appears to have several times found the embryonic hooks in young specimens of *Cysticercus pisiformis*, whose heads were still undeveloped.—R. L.]

becomes surrounded by a cellular layer which belongs to the host, and grows out posteriorly into a lappet. The hooks are then cast off, but may be observed for a while in the cellular layer, and the tape-worm head is developed within the embryo. These reports of Stein are unfortunately so far uncertain, that von Siebold thought himself justified in regarding the tail-like posterior appendage as an integral part of the worm. This seems all the more plausible, since it is on it that embryonic hooks are always found.[1]

So much the more grateful is it that we know other Cysticercoids which enable us to decide as to the relation of the six-hooked embryo to the bladder-worm.

Among these first and foremost is the so-called *Cysticercus arionis*, which is not unfrequently found in great numbers[2] in the pulmonary cavity of the red slug, and which originates from the *Tænia* of a bird, probably a red-shank (*Totanus calidris*). Meissner found here all the six hooks in their proper arrangement, but he so far misunderstood their position and the structure of the worm, that he overlooked the caudal bladder, and regarded the hooks which occurred at the passage of the latter into the neck as if they were at the posterior end. Such appearances as Meissner saw and figured are not unfrequently seen, but only when the body has been separated by pressure from the caudal bladder, which is all the easier since the cuticular covering of the latter possesses an unusual thickness and firmness, and is besides histologically very different from the former. If, after removing the surrounding connective-tissue cyst, one treat the worm for a short time with lukewarm water, the head can be seen stretched out, and the existence of an actual caudal bladder (Fig. 209, *B*) is placed beyond doubt. The latter exhibits under its cuticle a cellular layer, whose elements are of considerable size, and enclose a dull granular mass penetrated by fat globules, while the parenchyma of the tape-worm body seems to consist mainly of small clear cells, between which numerous muscle-fibres and calcareous bodies are embedded.

In its quiescent state, the body of the tape-worm is wholly retracted within the caudal bladder, so that the outer boundary is formed exclusively from the thick cuticle above mentioned (Fig. 209, *A*). The

[1] Moniez has indeed convinced himself ("Essai monogr. Cyst.," *loc. cit.*, p. 78) that the caudal appendage and the cyst of Stein belong to the *Cysticercus*, and therefore that the latter, essentially like a young *Cysticercus pisiformis*, lies naked in the body-cavity of the host.

[2] In one case I counted over a hundred *Cysticerci* side by side on the wall of the pulmonary cavity. See as to this worm especially my work on "Blasenbandwürmer," p. 115, where its structure is for the first time rightly described. The objections which Moniez has lately made (*loc. cit.*, p. 73) to my description apply only to matters of subordinate importance, and cannot all be regarded as settled points.

point of connection is seen as a narrow mouth-like opening, near which, in successful preparations, the embryonic hooks may be clearly seen. Since this is just the position at which the rudiment of the head first appears, one might suppose that the latter is formed also in the bladder-worms proper from the anterior hook-bearing segment of the embryo.

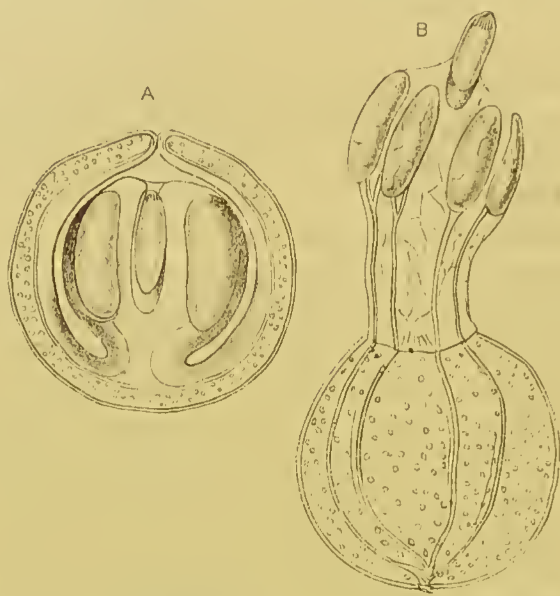


FIG. 209.—*Cysticercus arionis* with head retracted (*A*), and protruded (*B*). (× 50.)

The formation of the head has not, however, as yet been directly observed in *Cysticercus arionis.* This is the more to be regretted since the adult head is by no means a mere repetition of the ordinary *Cysticercus* type, but has its anterior end (with rostellum and hooks) always turned towards the place where the bladder was invaginated. It bears its suckers exposed on its outer surface. In position and attitude it thus resembles what we have occasionally seen, though only exceptionally, in the older bladder-worms (Fig. 201). Like the head of the future tape-worm, that of *Cysticercus arionis* seems to be a solid body, which fills up by far the greater portion of the caudal bladder, with which it is not, however, connected directly, but only by means of a cylindrical or sac-like connecting part—the future neck.

From the analogy of the *Cysticerci* just referred to, I think we may conclude that the head of *Cysticercus arionis* does not from the first appear in this attitude, but that it only assumes it in consequence of a change in the disposition of its parts. Here also I believe the development of the future tape-worm begins with the formation of a hollow bud, which starts from the wall of the enlarged embryonic body and grows into the loose interstitial tissue of the same. This does not become the sac-like and invaginated future neck portion in which the head is

only subsequently to originate; it begins from the first, as in the genuine forms, to become the head.[1] When the neck is formed the elevation begins to take place; the lower end of the sac, which has become the head, is pushed in like a plug into the other portion.

This pushing in of the head is a constant characteristic of these bladder-worms, and is not merely occasional, as may be established from a consideration of some features in the organization. In the *Cysticercus fasciolaris* of the mouse, in which the same mode of formation was observed, we referred the protrusion of the head to the considerable elongation of the connecting part; in *Cysticercus arionis* it is probably the elongated proboscis-like portion which bears the hooks that determines the protrusion. This supposition is confirmed by the fact that in all the other Cysticercoids with an elongated proboscis the same position and attitude of the head are found to obtain. Thus I find it, for example, in a Cysticercoid from the liver of *Lymnæus pereger*, which closely resembles the *Cysticercus arionis* in its whole organization, and which, from the structure of its hooks, may probably be referred to the *Tænia microsoma* of the wild duck. So is it also with the *Cysticercus* of *Tænia gracilis*[2] found by v. Linstow among the remains of small crustaceans in the intestine of a young perch, and in the *Cysticercus lumbriculi* found by Ratzel in *Sænuris variegata*,[3] which probably becomes *T. crassirostris* in the intestine of the snipe and other water-birds. The Cysticercoid forms of the *Tæniæ* of the shrew (*T. pistillum* and *T. scutigera ?*) lately described by Villot from *Glomeris*,[4] are also closely connected with *Cysticercus arionis* in the nature both of its head and of its rostellum.

FIG. 210. — *Cysticercus glomeridis*, after Villot. (× 50.)

There are, on the other hand, also Cysticercoids in which the rudiment of the head originates and grows in the typical bladder-worm fashion which we have formerly described. There are, as we should expect, forms with short rostellum, such as Nordmann's *Gypo-*

[1] Stein is the only investigator who has observed the first developmental stages of a Cysticercoid. Speaking of this process he says—"The further changes of the encysted embryo are as follows: an ever-deepening depression is formed at the truncated anterior end, and the head, with its proboscis and suckers, is at the same time formed in the centre of the embryonic body from the absorbed ground-substance," *loc. cit.*, p. 210. The accompanying figures show in Tab. x., Fig. 13, a *Cysticercus* with invaginated portion and rudiment of head, whose hooks are hardly raised as far as the middle of the bladder body, while they are afterwards found close behind the point of invagination.

[2] *Archiv f. mikrosk. Anat.*, Bd. xxi., p. 535, 1871.

[3] *Archiv f. Naturgesch.*, Jahrg. xxxiv., Bd. i., p. 147, 1868.

[4] "Migrations et métamorphoses des Ténias des Musaraignes," *Ann. Sci. nat.*, ser. 6, t. viii., Art. 5, 1878; also *Ann. Mag. Nat. Hist.*, ser. 5, vol. i., p. 258.

rhynchus, with which we have become more intimately acquainted through Aubert,[1] and also the young form of the *Tænia cucumerina* of the dog.

Two closely related species of the former live in the tench—the one between the intestinal villi, the other in the gall-bladder; in situations, therefore, which are only rarely inhabited by young Helminths. They exhibit, also, a habit very unusual for a bladder-worm, namely, that of occasionally stretching the head out of the caudal bladder and creeping about inside their place of abode, like an adult tape-worm. Even in this state, however, the adherent caudal bladder, which is sharply separated from the rest of the body both externally and histologically, attests undeniably their Cysticercoid nature. To reach their adult state, they have to pass into the intestine of the heron, where, according to Krabbe, they are to be recognised by the characteristic structure of the hooks, as *Tænia macropeos* and *T. unilateralis*. As to the position of the head in the invaginated state there can be no doubt, after Aubert's description and figures.[2] "The points of the hooks are," he says, "turned towards the posterior end of the animal, while the central fixed portions lie towards the unfolding of the fat-sac (*i.e.*, towards the point of invagination of the caudal bladder), and towards the same point between it and the circle of hooks lie the suckers." All this agrees exactly both with the formation of a typical *Cysticercus* and with the state of affairs in the Cysticercoid of *Tænia elliptica* (= *T. cucumerina*), which, as is well known, undergoes its development in the body-cavity of the dog-louse (*Trichodectes canis*) (Fig. 211).

Fig. 211.—Cysticercoid of *Tænia cucumerina* (× 60).

The latter may be ranked by the side of *Gyporhynchus*, on the ground of the morphological similarity between the two. Both arise in similar fashion from a sac, and from a *Tænia*-head invaginated therein. The resemblance, however, stops here; for, in their further relations, the two forms differ widely. This is the case at least with the external body, which we have just called the "sac." In the *Gyporhynchus* this exhibits a distinct caudal bladder, as in the other Cysticercoids which we have discussed. This bladder is in form and histology sharply distinguishable from the rest of the body, and retains its independent character even in the outstretched state. In the *Cysticercus* of *Tænia elliptica*, however, the bladder seems in

[1] *Zeitschr. f. wiss. Zool.*, Bd. viii., p. 274, 1857.
[2] *Loc. cit.*, p. 285, Tab. x., Fig. 7.

appearance and character simply as a process from the head-bearing anterior end, belonging to it much in the same way as the neck portion of an *Echinococcus* to its head. Here we find in an exaggerated degree the same structure as we formerly noted in regard to the "parenchymatous *Cysticerci*."

It seems doubtful whether we can refuse to recognise at least the genetic identity of the sac-like external body of this *Cysticercus* with a caudal bladder, especially since the results of the discoverer's [1] investigations, which were controlled and corroborated by myself, make it probable that the subsequent external body is formed directly from the six-hooked embryo. The details of the development are unfortunately unknown; we only know that the immigrant embryos, before the loss of their hooks, grow to about half the size of the Cysticercoid, and change their original shape for a somewhat pear-like form. The embryonic hooks are not to be found on the adult Cysticercoid.

We must, moreover, admit the possibility of the young tape-worm being developed by a simpler process than through the Cysticercoid form. I am led to this admission partly by a communication of Dr. Gruber's in regard to a young *Tænia*, which he has since described elsewhere, and which he found in investigating the littoral fauna of the Boden See.[2] It was a worm about a millimetre long, which was found stretched out in the body-cavity of *Cyclops serrulatus*, occupying almost the whole space above the alimentary canal between eye and abdomen. Special parts could hardly be distinguished; the body consisted of a clear mass, with uniformly diffused calcareous bodies; it had a simple cylindrical form, and was furnished at the somewhat

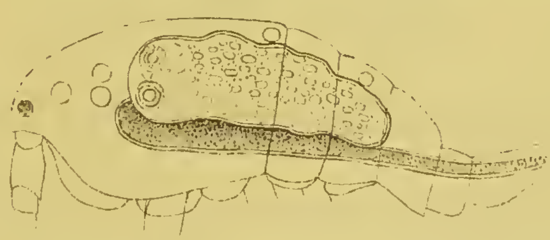


FIG. 212.—Young form of *Tænia torulosa* (?) in *Cyclops serrulatus*, after Gruber. (× 25.)

thickened, hookless, anterior end with four distinct suckers. In the great multitude of infected *Cyclops*, it was difficult to find the previous stages. None of these, however, had the form of a *Cysticercus*. They

[1] Melnikoff, "Ueber die Jugendzustände der Tænia cucumerina," *Archiv f. Naturgesch.*, Jahrg. xxxv., Bd. i., p. 69, 1869.

[2] *Zool. Anzeiger*, Jahrg. i., p. 74, 1878.

were all simple, round, or pear-shaped bodies, some of very minute size, which seem to pass directly by growth and formation of suckers into the definite larval form. Their origin is uncertain, though Gruber suggests their connection with the hookless *Tænia torulosa* of our white fish. This is corroborated by the fact that I once found a number of young *Tæniæ* in the intestine of a loach, which perfectly agreed in size and appearance with the forms described by Gruber, and in addition to the calcareous corpuscles also exhibited four coiled vessels running down the body.

The demonstration of the nature and history of the ordinary Cysticercoid condition does not, therefore, complete our knowledge of the development of the *Tæniæ*, as is further evidenced by the observations made by Mecznikoff in Odessa on a parasitic "*Echinococcus*-like" larval stage of an otherwise unknown twelve-hooked *Tænia*.[1] This *Echinococcus*-like form was found in the body-cavity of the common earth-worm. In its mature condition it consists of a thin-skinned bladder (Fig. 213, *E*), which contains a varying number (up to thirteen) of small *Cysticerci* of about 0·5 mm. in diameter.

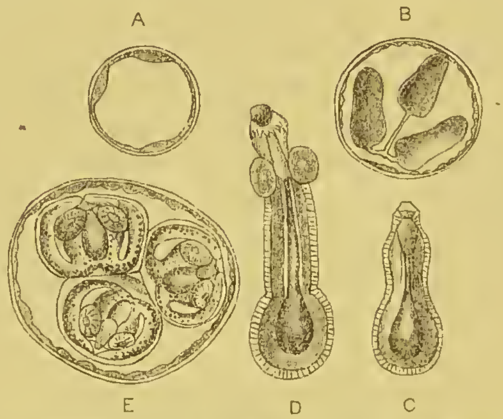


FIG. 213.—Development of an *Echinococcus*-like Cysticercoid from the body-cavity of the earth-worm, after Mecznikoff. (× 25.)

Although the latter lie quite free in the interior, and possess, like the ordinary Cysticercoids, the distinctive caudal bladder, they are of very unusual origin, inasmuch as, instead of developing directly from the six-hooked embryos, they arise by proliferation of the wall of the surrounding bladder (Fig. 213, *B*). The bladder is thus the brood-capsule of the enclosed Cysticercoids, and corresponds in some respects to the brood-capsule of the *Echinococcus*, or perhaps to a

[1] *Verhandlungen d. Petersburger Naturf. Versamml., Zool.*, pp. 263-266, 1868 (in Russian). The worms were given to ducks, but without result. According to the structure of their hooks they close resemble, if they be not identical with, *Tænia nilotica*, Krabbe, from the intestine of *Cursor isabellinus*.

Cœnurus-bladder, and, like these, is undoubtedly to be referred to the six-hooked embryo. The first developmental stage observed by Meczuikoff appeared to be a solid ball of about 0·08 mm., with an unusually thick cuticular envelope and cellular contents. The latter subsequently become clear on attaining a diameter of 0·14 mm., when the embryo lies upon the inner surface in the form of a cellular layer. Soon the buds begin to form, and that exclusively from the cellular wall, which becomes thicker at certain spots, and sends little projections (*A*) into the inner cavity. Although at first flat, and connected by their broad bases with the cellular wall, the protuberances, as they grow larger, gradually detach themselves from the subjacent layer. This separation is facilitated by the development of a hollow space in the interior of the basal portion,[1] so that after a time the bud is only connected with the mother-bladder by a thin filament (*B*). Finally, this connection is destroyed, and the bud thus becomes an oval body lying freely in the interior. It then proceeds to undergo its further development. This is essentially the same as that which we have already served in the buds situated inside the brood-capsule in the *Echinococci*, only that in this case not only head and neck are formed, but a third joint, consisting of a kind of caudal bladder. All these parts are formed almost simultaneously, for the originally compressed and solid bud increases in length, then becomes hollow inside, and becomes jointed by the development of the hook-apparatus in front and a bladder-like expansion behind. When the suckers and hooks[2] are completely developed (*D*), the anterior part of the body draws back into the caudal bladder by invagination of the neck, so that at the end of its development the worm has exactly the same position as we formerly observed in *Cysticercus arionis.*

The short description which we have given of this wonderful *Tœnia* form by no means exhausts the similarities which sometimes exist between the Cystercoids and the *Echinococci.* The former are not only capable of internal proliferation, but in some cases multiply also by external buds.

Villot observed this process in the already mentioned Cysticercoids of *Glomeris*, where it was so often repeated, that the parasites assumed quite a racemose appearance, from which fact, indeed, he has named these forms "Staphylocysts." In this form they may be seen hanging together in dozens (Fig. 214, *A*) in the ureter of their host. Such a colony contains larger and smaller, younger and older bladder-worms,

[1] Mecznikoff inaptly compares this hollow space to the interior of a brood-capsule.

[2] Although the rudimentary hooks are in a double row, the definitive hook-apparatus consists only of a single circle, for the rudiments of the second circle become abortive, and disappear.

at different stages of development, and all hanging together by means of a thin stalk at the posterior end of the caudal bladder. Here, too, of course occurs the formation of the buds, which at first are nothing else than accumulations of cells, which force their way out, and are surrounded by a continuation of the cuticle. It is unnecessary to give any account of the metamorphosis of the buds, since to do so would only be to repeat what we have already noted in the case of *Cysticercus arionis* regarding the structure of the tape-worm head and of the later caudal bladder; for in this case the bud is nothing else than a repetition of the six-hooked embryonic body.

FIG. 214.—*Cysticercus glomeridis* (after Villot). *A*, Two groups of bladder-worms produced by proliferation (under low power); *B*, *Cysticercus* in its natural position; and *C*, with evaginated body. (× 200.)

After these observations, it cannot be doubted that the development of the *Tæniæ* follows, on the whole, the same type in the higher and lower forms. With the exception of a few somewhat doubtful cases, this is true throughout of the Cysticercoid state. It is true that many differences occur in the size and nature of the bladder; but however remote certain species may be from each other, they are always connected by intermediate forms. Consequently, the difference which we formerly established between the true bladder-worms and the Cysticercoids becomes a distinction of somewhat doubtful value.

On the other hand, it must not be overlooked that the apparently "dropsical" nature of the bladder in the genuine bladder-worms constitutes a very remarkable and striking peculiarity, and all the more

striking since we can give no plausible explanation of it. It might certainly be supposed that the watery contents of the bladder formed a nutritive fluid, if this idea were not excluded by the extremely small quantity of nutritive material which it contains (0·2 to 0·3 per cent. of albuminoids,[1] and 0·03 to 0·05 of fat). Neither does the chemical analysis of the water of the bladder show it to be an excretory product; for it yields, apart from the above substances, a weak saline solution (with about 3 per cent. of salts, mostly of soda).

Under these circumstances, there is hardly any alternative but to regard the collection of water as an arrangement for securing certain individual advantages. Perhaps in this way a more favourable, that is to say an increased, absorptive surface is furnished to the parasite, or perhaps greater protective needs are thus met. A fact—possibly of importance in this last respect—is that the genuine bladder-worms are apparently exclusively confined to the Mammalia, so that some protective arrangement is therefore very necessary to them, on account of the size and motions of their hosts. The theory that the effects secured by the apparent dropsy are of a mechanical nature, seems the more plausible since similar arrangements have occasionally been observed to fulfil similar functions in the Graffian follicles, in the amnion, and in the eye.

But when we use the term "bladder-worm" in a wider sense than the older Helminthologists did, we note at once that the presence of this developmental phase is by no means limited to the *Tæniæ*, but occurs on the whole almost universally among the Cestodes. One has only to cast a glance over the often-quoted treatises of van Beneden and Wagener to notice large numbers of such forms in the most diverse families of tape-worms. Even Rudolphi observed this structure in a few of these bladder-worms. The forms which he mentions belong exclusively to the marine group of the *Tetrarhynchi*, and, from their size and occurrence in the muscles and in the parenchymatous viscera (in fishes), must be allied to the genuine *Cysticerci*. These worms could not of course be ranked with the genus *Cysticercus*, for the form of their heads was quite different ("caput bothriis 2 vel 4 et proboscidibus uncinatis 4 instructum"). They were therefore regarded as the representatives of a distinct genus, *Anthocephalus*, which, by the structure and armature of its head, recalled certain *Bothriocephali* living in the intestines of rays and sharks (now called *Tetrarhynchi*, Rudolphi's *Rhynchobothrii*), just as the other bladder-worms recall the *Tæniæ*.[2]

[1] It is on account of this small quantity of albumen that the bladder-fluid can be coagulated neither by boiling nor by the addition of acids.

[2] Nitzsch in Ersch and Gruber's "Encyclop.," Art. *Anthocephalus*, Bd. iv., p. 259, 1820.

On the other hand, it is true that the Cysticercoid nature of the *Anthocephali* has been doubted. My uncle F. S. Leuckart explained the latter, in opposition to Rudolphi, as young *Tetrarhynchi* (or *Bothriocephali*), and denied the interpretation of the surrounding bladder as a caudal bladder, since even in examples sent by Rudolphi (*A. gracilis*) both Bremser and he found the posterior end of the tape-worm free and without any connection with the surrounding bladder, and could not perceive any rupture in it.[1] We now know that both investigators were right.[2]

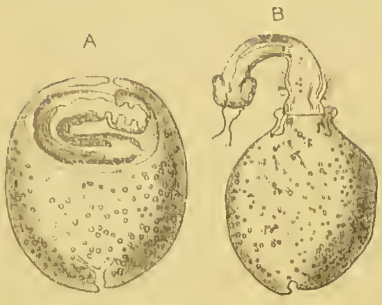


FIG. 215.—Cysticercoid *Tetrarhynchus* from a Mediterranean Percoid. *A*, in its natural position; *B*, with evaginated body. (× about 20.)

In spite of their considerable size, the *Anthocephali* belong, however, to the parenchymatous bladder-worms. Instead of water, they contain (see Fig. 219) an areolar connective tissue, which fills the whole of the interior, and is in continuous connection with the external envelope of the body.[3] This circumstance also explains how the *Anthocephali*, and especially the larger ones, instead of developing into balls, stretch out longitudinally, and sometimes assume an almost tape-worm-like form. This is most striking in the species (*Anthocephalus s. Gymnorhynchus reptans*) living in the muscles of *Brama Raji*, which in course of time becomes a ribbon almost a yard long, and only exhibits a ball-like swelling near the anterior end where the receptaculum with the head is placed.

The appearance of the head after development is always the same as in the adult tape-worm. It forms a solid mass with outwardly directed suctorial pits, and, as in the majority of the Cysticercoids, is raised like a plug from the floor of the receptacle with which it is at first always in continuous connection (Fig. 215). In many species this connection is permanent, so that the receptacle distinctly appears as an integral portion of the tape-worm, like the evaginated neck, which, in the other Cysticercoids, is generally the means of connection with the caudal bladder. In other species, however, the former connection is dissolved when the head is perfectly developed, and then the latter lies quite free in the interior of the former neck, as my uncle quite correctly observed within the first twenty years of

[1] *Zoologische Bruchstücke*, Heft i., p. 67, 1819.

[2] See in regard to this v. Siebold's "Abhandlung über den Generationswechsel der Cestoden," *Zeitschr. f. wiss. Zool.*, Bd. ii., p. 200, 1850, and van Beneden, *Mém.*, &c., p. 76.

[3] Hoek, "Ueber den encystirten Scolex von Tetrarhynchus," *Niederländ. Archiv f. Naturwiss.* 1879.

this century. In such cases the free posterior end has usually a thick fringe of hair-like spines, just as in the *Tetrarhynchi* the rest of the body is frequently covered to a large extent with small closely set bristles.

Not unfrequently this separation of the head leads in course of time to a complete emigration. Not only are *Tetrarhynchus*-bladders frequently found forsaken by their inmates, but also *Tetrarhynchus*-heads occur in places and in animals in which the other stages of their development are sought for in vain. Of the numerous cases of this kind (all those forms which Rudolphi originally enumerated in his genus *Tetrarhynchus* consist simply of these isolated heads) I shall only mention[1] the *Tetrarhynchus*-heads found in the muscles of *Sepia* (*T. macrobothrius?* Fig. 216), which sufficiently reveal their origin by the hair-like fringe at the posterior end, and have already been frequently observed by former investigators (Rudolphi, delle Chiaje, Wagener, &c.). At one time they are found boring and digging between the fibrous bundles of the mantle, and at another time quiescent, and then surrounded by a thin envelope of connective tissue, but always at the same stage of development. Only in size do they exhibit any marked difference, for some have double the diameter of others, but this amounts to nothing more than that these inmates have remained in their host for a different length of time. The latter are not, of course, to be regarded as the final hosts. They play the part of intermediate hosts, and only affect the life-history of our parasite, in so far as they extend its distribution and facilitate or render possible the subsequent transference.

FIG. 216. *Tetrarhynchus sepiæ* (× 12).

It also looks as though the *Tetrarhynchi* furnished by no means the only example of such a change of hosts.

Young unjointed Cestodes, not unlike isolated heads of *Tæniæ*, have long been known to inhabit the intestines of many sea-fish. These have a so-called "frontal sucker," more or less highly developed between the other four suctorial pits, and not unfrequently also two red eye-spots behind the hook apparatus. Rudolphi founded a special genus (*Scolex*) for these animals, and thought that they ought all to be regarded as representatives of a single species (*S. polymorphus*).

Thanks to the investigations of Wagener and van Beneden, we have, however, become more thoroughly acquainted with these parasites. We now understand not only how to distinguish the different species, but also know that these gradually change the originally simple structure of their suctorial cavities for a more complicated

[1] According to a communication of v. Ihering, the genus *Tethys* may be added to the number of the animals in which these parasites are known to occur.

one, and ultimately become forms, which were formerly like the *Tetrarhynchi*, ranked among the *Bothriocephali*, but since the time of van Beneden have been more correctly described as *Phyllobothria* (in the widest sense of the word). The adult worms live, like the *Tetrarhynchi*, principally in rays and sharks.

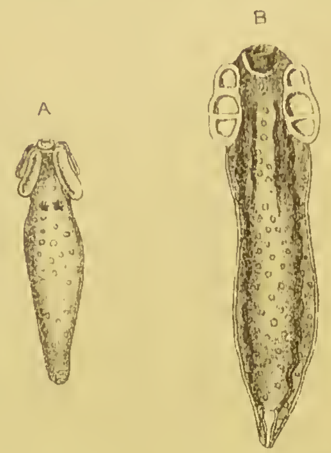


FIG. 217.—*Scoleces*: *A* from the intestine of *Sepia* (after van Beneden); *B* from *Lophius piscatorius*. (× about 30.)

Thus I think I am now entitled to regard these *Scoleces* as structures parallel with the wandering *Tetrarhynchus*-heads; and this all the more decidedly since they not only live in a wandering state in very different animals (besides fishes, in Cephalopoda, snails, and Ctenophora), but are also frequently observed swimming about in a free state.[1] In the frequent possession of eye-spots, we might even see an arrangement which specially adapts these animals for active wandering.

The parallel would be perfect if we could show that these *Scoleces* originated, like the *Tetrarhynchus*-heads, in the interior of a bladder. And indeed it cannot be doubted, after the observations of van Beneden, that there are *Phyllobothria*, which pass through a Cysticercoid larval state (*Phyllobothrium lactuca* and *Acanthobothrium coronatum*).[2] But it appears as if these observations referred only to such Cestodes as retain their early state until they are transferred to their final host. At any rate the forms observed by van Beneden exhibit even as bladder-worms in the appearance of their suckers a very close approximation to the subsequent state. A similar structure is found in a Cysticercoid of a *Phyllobothrium* (*Echeneibothrium ?*) which Wagener found in the large intestine of a *Trygon*. "Like a *Tetrarhynchus*, the animal was suspended by threads in a sac within its caudal bladder. Its head had hairs and its neck red spots. The bladder was burst by pressure and the animal was set free. There

[1] Claparède twice fished a *Scolex* of this sort out of the sea, and quite correctly concluded that a "normal migration" occurred, ("Beobacht. über Anatomie u. Entwickelungsgesch. wirbellose Thiere," p. 14, 1863.) The animals possessed four suckers with double cups (Bothria bilocularia), and swam by a snake-like motion of the whole body. Panceri found a similar *Scolex* on the skin of *Brama Raji* ("*Rendiconto Accad. Napoli*, February 1868).

[2] With this ought to be ranked Rudolphi's *Cysticercus delphini*, which was till lately referred to the *Cysticerci* proper; see P. J. van Beneden, *Bullet. acad. roy. Belg.*, t. xxix., p. 360, 1870.

were no joints to be seen. Its lower end was still firmly attached by a thread to the caudal bladder which collapsed."[1] The description indeed suggests that the head was in this case destined to be set free, and to wander on its own account, but from the complicated form of its suckers it could hardly be regarded as a *Scolex* in Rudolphi's sense of the term.

Under these circumstances, then, there is little support for the supposition that the *Scoleces*, with which we formerly became acquainted, are to be interpreted as the isolated heads of a Cysticercoid developmental stage. It is, of course, conceivable that such a relation may be afterwards proved, but we ought to bear in mind the possibility that, unlike what is the case in *Tænia cucumerina*, the apparent heads may be regarded as Cysticercoid forms with appended, although not histologically differentiated, caudal bladders.

This is a view which essentially coincides with the idea which we find, though unformulated, in Wagener's excellent treatise on the development of the Cestodes.[2] What led him to it was at first only the presence of a "pulsating tube" opening at the posterior end of the body. This organ he regards as a characteristic peculiarity of the caudal or Cestode bladder ("the head-former"), which springs from the hooked embryo, and he further proves the existence of this developmental stage in numerous cases, and always in connection with a more or less complicated and often ciliated vascular apparatus. Of no less significance is the fact that Wagener frequently found the *Scoleces* "with heads drawn back" (compare the illustrations in Tab. ix. of his work), that is to say, in a position which so perfectly corresponds with the already mentioned *Cysticercus Tæniæ cucumerinæ*, that one cannot refrain from collating the two forms. It is certainly striking and unusual in a Cysticercoid form for the *Scoleces* to live free and mobile in the intestine of their host, but in *Gyporhynchus*, also found in fish, we find this in an unmistakeable Cysticercoid.

If our idea be correct, then there are Cysticercoid forms among the *Phyllobothria* as well as among the *Tæniæ*, whose caudal bladder is both anatomically and histologically an integral portion of the head, being developed inside it, and being sometimes subsequently drawn back into it.

In this retracted state the head of the *Scolex* is in exactly the same position which we formerly found that organ occupying in the *Cysticercus* of the dog-louse, and which we then considered as mainly characteristic of the bladder-worms. The drawings which

[1] *Loc. cit.*, p. 58.

[2] Van Beneden also directly mentions the above-mentioned *Cysticercus* of *Phyllobothrium lactuca* and *Acanthobothrium* as a *Scolex* (*loc. cit.* pp. 73, 74).

Wagener has made of it (see especially Fig. 111 of his work) leave not the slightest doubt on this point. According to the description of van Beneden, a similar appearance is found in the *Cysticercus* of *Acanthobothrium coronatum*. The cavity of the suctorial cups is always directed towards the interior of the invaginated cavity, and the future crown is situated meanwhile as far back as possible on the rudimentary head.

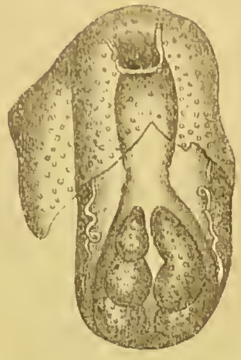


FIG. 218.—Larva state of *Acanthobothrium coronatum*, after van Beneden. (× 25.)

In contrast to this, however, the head of *Tetrarhynchus*, &c. is said not to originate directly from the first sac-like structures, but to be subsequently developed in the interior, by the base rising up into a thimble-like projection, inside which the different organs of the head are formed. "If we imagine the thimble-like projection from the base of the sac broadened out above like a mushroom, we have the head of a *Dibothrium*, which might become a "dibothrian" *Tetrarhynchus* by the addition of proboscides." So we read in Wagener,[1] and van Beneden says pretty much the same thing, but differs in so far as he takes the *Scolex*-form for his starting-point (see p. 329), and does not regard the head-sac as a new structure, but the retracted anterior end of the worm.

After the foregoing observations, it cannot be doubted that in the *Tetrarhynchi* and the related forms the base of the originally quite simple[2] head-rudiment is raised into a boss-like elevation to effect the formation of the head proper. But of course that does not imply that these plugs alone produce the head. This is by no means proved by the preceding statements, for these all rest upon investigations which are quite insufficient to establish any such conclusion.

In order to study more especially the process of the formation of the head, I have investigated by means of sections a number of young *Tetrarhynchus*-bladders from the muscle of *Lophius piscatorius*. The material certainly furnished me with no continuous developmental succession, but it convinced me most distinctly that the elevation only takes place at a time when the suctorial cups and proboscides are already formed, and when the head, with its different parts, is thus essentially mature. Upon the whole, the conditions are quite similar to those of the typical bladder-worms.

[1] *Loc. cit.*, p. 52.

[2] In claiming this rudimentary head as simply a hollow bud, I do so not only on the ground of Wagener's statements, but on the basis of my own investigations of *Tetrarhynchus* and *Echinobothrium*.

As in these, the suctorial cups at first lie in the wall of the rudimentary head, close in front of the posterior cæcal end, so that their cavity is directed inwards. Between them there is as yet but a slight elevation, which scarcely rises to the height of the suctorial cups, and covers itself with the lower muscular borders of the latter. On the anterior borders of the same may be noticed the opening of the proboscis-sheaths, which extend back along the floor of the cæcum with their invaginated hooks and terminal pouch, and which are externally covered by the receptacle-like muscular sheath surrounding the rudimentary head. At the anterior border the fibres of this sheath may be observed bending round into the peripheral musculature of the Cestode-bladder, which is filled inside with large granular cells.

FIG. 219.—Longitudinal section of a still imperfectly developed *Tetrarhynchus* from the muscle of *Lophius*. (× 25.)

We thus get the same result in regard to the *Tetrarhynchi* as we formerly did from our investigations of the *Tæniæ*, and they may be summed up thus,—that it is the sac-like invagination of the bladder itself which produces the head. The elevation always appears only as a secondary structure of subordinate morphological importance, and is, moreover, by no means so widely distributed as the statements of some investigators would lead one to suppose.

All the Cestodes which we have as yet considered, in spite of their other differences, agree in being provided with a well developed "head," which is in form and structure in sharp contrast to the rest of the body. But, besides these, there are a number of Cestodes with a simple, more or less inconspicuous head, which is as a rule provided with two superficially situated longitudinal pits,—a circumstance which has procured for these animals the name of "Dibothria." Like the head, the segments are less individualised, being not unfrequently indicated only by the successive repetition of the sexual organs (*Ligula*, *Triænophorus*), or even represented by a completely simple body (*Caryophyllæus*, *Archigetes*). The genus *Bothriocephalus* (*sensu stricto*) is the first of this group,—the only tape-worm outside the genus *Tænia* which is found in man.

Such being the case, a special interest naturally attaches itself to these tape-worms. All the more is it to be regretted that our experience of the forms in question is hitherto only slight. It is true that we are acquainted with a number of young Dibothria in the higher

and lower animals, especially in fish, which live like bladder-worms in the muscles and in the parenchymatous organs, or occasionally free in the body-cavity (*Schistocephalus*, *Ligula*); but their mode of development has not been observed, or at least not traced as far as the hook-bearing embryo. The only form which we must except is the peculiar genus *Archigetes* — peculiar, because while as yet in the Cysticercoid condition, or at least while still possessing the attributes of an embryo, it becomes sexually mature, and that too (the only example in the Cestodes[1]) in an invertebrate animal (*Sænuris* and its allies). The development is further very simple in this case, for the six-hooked embryo becomes transformed into the adult animal without interruption or change of abode. During its continuous growth it exchanges its original form for a more club-like one, and by modification of the anterior as well as of the posterior portion, becomes a tail-bearing worm, which at first sight has a striking resemblance to a *Cercaria*. The embryonic hooks persist at the posterior end of the caudal appendage, and the modification of the embryo, which has at first the usual structure, is effected mainly by the distention of the segment opposite the hooks, while the rest of the body preserves its slender form, and ultimately grows out into a long appendage. This tail-like appendage is thus the direct developmental product of the six-hooked embryo. In spite of its dissimilar form (we have, however, found a similar one among the *Tetrarhynchi*) it is homologous with the bladder of the other Cestodes. Like the latter, it plays in the *Archigetes* the part of a "head-former," for the protuberance out of which the head-bearing body of the worm arises might after all be regarded as a bud-like proliferation, just as is the head-rudiment in the bladder-worms. The fact that this bud does not grow as usual inside the (increased) six-hooked embryo, but is appended exteriorly, cannot constitute a difference, since both external and internal buds occur promiscuously in the animal kingdom. It is true that in this case there originates from the bud, not a head merely, which afterwards forms the segmented body by new budding, but a structure which, from the first, exhibits both head and body; for the anterior

FIG. 220.—*Archigetes Sieboldi* (× 60).

[1] The significance of this fact, to our conception of the historical development of parasitic life, has already been noted (p. 70). Compare also, regarding this interesting form, Leuckart, *Zeitschr. f. wiss. Zool.*, Suppl.- Bd. xxx., p. 593, 1878, and Ratzel, *Archiv für Naturgesch.*, Jahrg. xxxiv., Bd. i., p. 138, 1868.

end, like a head, bears the two suctorial pits, while the rest of the body develops the sexual organs. What is in the other Cestodes spread over two successive generations, seems in *Archigetes*, as well as in some other forms, to be condensed into a single developmental stage; for the animal is not a colony with head and sexual animal, but a simple head-bearing and sexually mature flat-worm.

According to all appearance, this is, however, not the only Cestode which develops in the manner described. Wagener[1] tells us that in *Triænophorus*, so long as it remains encapsuled in the liver of the fish—that is to say, lives in its intermediate host—there is seen attached to the thick fore-part of the body, which bears the attaching apparatus (pits and hooks), a ribbon-like caudal appendage, almost half as long as the entire body. Bounded in front by a constriction, and very different in structure from the rest of the body, it is dragged about by the motions of the animal like a lifeless mass. It is thus undoubtedly a peculiar structure, and comparable to the caudal bladder of the other Cestodes, in so far as it is at first destitute of the fore-part of the body, and itself represents the worm.

In the other Dibothria, so far as we know, a special caudal appendage is never present. The embryo apparently grows by simple elongation into a cylindrical or tape-like worm, which then forms the attaching apparatus at its anterior end, in a way which has not yet been ascertained. These developmental processes have a general resemblance to those which we formerly saw to be characteristic of Rudolphi's *Scoleces* (and other Cysticercoids), only that in this case the share which the embryo takes in the formation of the adult animal is much more than merely structural.

FIG. 221.—Larva of a *Bothriocephalus* from the smelt.

In many cases the Dibothrian tape-worm attains, even in this intermediate stage, a considerable size. Thus Diesing[2] describes, under the name of *Spargarum reptans*, what was probably nothing else than a larval form of *Bothriocephalus*, which was a foot long, and occurred in no fewer than thirteen mammals, twenty-four birds, and fifteen amphibians, all in Brazil. It was sometimes encysted under the skin, or between the muscles, and sometimes occurred free in the

[1] *Loc. cit.*, p. 26 *et seq.* Zeder, however, made the same observation before Wagener ("Nachtrag zu Göze's Naturgesch.," p. 414). He was even led by it to rank this worm (as *Vesicaria lucii*) with the *Cysticerci*.

[2] *Denkschriften der Wiener Akad.*, Bd. ix., tab. ii., p. 174, 1855.

body-cavity.[1] The strap-worms (*Ligula*) which inhabit the body-cavity of our freshwater fish attain a still larger size, and also advance further in development, since they form their sexual organs while still in their intermediate host. The same is true of the *Schistocephalus* of the stickleback, which is, upon the whole, very nearly allied to the strap-worms, and is indeed only distinguished from them in this, that the tape-like body is externally jointed, and that this segmentation takes place during the larval state.[2]

It will thus be understood that the hosts of the Ligulidæ are endangered in a high degree by the growth of their parasites. In nearly every case their parasitism results in a chronic peritonitis, to which large numbers of fish fall victims. There are even distinct instances of epidemics being caused by these worms, and especially by *Ligula*.[3]

It might, however, be doubted whether the Ligulidæ live from the first in the body-cavity. At any rate one finds not unfrequently in the liver of their host Helminth-capsules, enclosing a young, still undifferentiated, Cestode of simple shape, which might quite well be the larval form of *Ligula* or *Schistocephalus*. In this case transference into the body-cavity would of course soon follow, since only a few weeks after infection with ciliated embryos (apparently introduced through the intestine, and not through the skin) Donnadieu[4] found young strap-worms in the body-cavity. Although some of them were only from six to seven millimetres long, they possessed essentially their subsequent structure.

So far as we know, there is no other Cestode besides *Archigetes* which completes its development without interruption or change of host, or, what is the same thing, becomes sexually mature in its first host.[5] And we can indeed hardly count *Archigetes* an exception,

[1] From the manifold nature of the hosts alone it is very improbable that all these worms belong to the same species (see p. 12).

[2] It is true that when we remember that the true Ligulidæ, and especially the still small young specimens, also exhibit distinct traces of segmentation, this difference becomes only one of degree.

[3] See Donnadieu, "Contributions à l'histoire de la Ligule," *Journ. anat. et physiol.*, p. 321, 1877.

[4] *Loc. cit.*, p. 452.

[5] Even on this ground the assertion of Knoch that, in the human intestinal canal, *Bothriocephalus latus* develops from the six-hooked embryo (even from the undeveloped egg!) directly into the later tape-worm, has only slight probability. When describing the worm more specially we shall afterwards return to the views and experiments of this author ("Naturgesch. des breiten Bandwurmes," *Mém. Acad. St. Petersb.*, t. v., No. 5, 1862), but it may now be mentioned that the experiments on which Knoch founds his assertion have by no means the cogency which he fancies. [Braun of Dorpat has shown experimentally, as we shall see hereafter, that *Bothriocephalus latus* has an intermediate host in its young stage, just like other Dibothria, and that its larva is transferred

merely because it attains in the Cysticercoid condition that maturity which is in other cases only reached at a later stage of development—wanting in *Archigetes*. In order to attain this definitive developmental stage the tape-worms must be transferred from their former host to some other suitable animal. Along with their hosts, or with the portions which they inhabit, they are imported into the intestine of a new host, where, after greater or less alterations, they become adult tape-worms. With the exception of *Archigetes*, the sexually mature Cestodes occur only in the vertebrates.

The transition into the sexually mature worm occurs most simply in the Ligulidæ, which, as larvæ, are already comparatively mature, and have their sexual organs even then almost completely developed. Twenty-four hours after they have passed into the intestine of a duck or some water-bird, one finds them with eggs fully developed, provided of course that they previously possessed the requisite differentiation and size (at least 10 cm.).[1] In other cases the worms are digested, or are expelled unchanged with the fæces. Even in their sexually mature state the Ligulidæ remain but a few days in the alimentary canal of the bird; after the course of a week or even earlier they succumb to the same fate as the larval forms, being either expelled or altered by digestion, which first affects the posterior end. Donnadieu estimates the average duration of the parasitism of Ligulidæ only at two and a half days. In water of ordinary temperature these animals remain living for eight or ten days. As regards their external appearance, the only change on the acquisition of sexuality is the considerable elongation and narrowing of the body.

In the case of the isolated *Tetrarhynchus*-heads, the progress of events is somewhat more complicated. After they have been transferred, along with their intermediate host, into the alimentary canal of a shark or ray, the passage into the final stage is accom-

to man from fish, especially the pike.—R. L.] I may also remark that Mégnin and Moniez have lately maintained for the *Tæniæ* a continuous development without change of host and without cystic state—a supposition based essentially on the fact that the number of known bladder-worm forms is much too small in proportion to the great number of the existing species of tape-worms. They forget that the tape-worm hosts often devour hundreds of animals before they find a bladder-worm host; in other words, that the bladder-worms are very sparsely distributed, especially in the lower animals, and therefore often escape our investigation. At any rate this assertion is not worthy of much consideration until it is established by direct observations.

[1] See Donnadieu, *loc. cit.*, and Duchamp, *Ann. sci. nat.*, t. vii., No. 7, 1876. The latter observed the attainment of sexual maturity even in some worms transferred experimentally into the body-cavity of a dog (*Comptes Rendus*, t. lxxxvi., p. 493, 1878). It can therefore hardly be doubted that it is primarily and principally warmth which brings them to ripeness; nor is it necessary to have the whole worm—even separate pieces become ripe in the intestine of the bird.

plished by means of the growth and segmentation of the cervical portion adherent to the head, by a process, therefore, which gives the parasite an entirely new stamp, and converts it indeed into a perfect tape-worm. Rudiments of this segmentation are even often to be seen during the stay of the parasite within the intermediate host. Thus at least in a *Tetrarhynchus*-head from the gills of *Lepidopus*, which in some points recalled *T. lingualis*, but measured only 4 mm., I observed that the neck, in spite of its perfectly simple external appearance, was also characterised by a distinct segmentation resulting from the internal arrangement especially of its vessels and muscles. In thin longitudinal sections I could count about two dozen narrow segments, which gradually became somewhat longer posteriorly, and even revealed the first traces of the sexual organs.

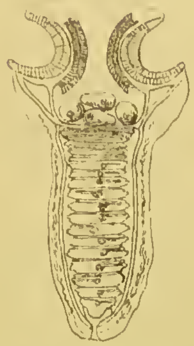


FIG. 222. — Longitudinal section of an isolated head of *Tetrarhynchus*. (× 10.)

But it is not only the isolated *Tetrarhynchus*-heads which grow into the future tape-worms in this directly simple fashion. The same may be said of the worms formerly described as *Scoleces*, and of all those Cestodes which are in their larval state destitute of a histologically differentiated caudal bladder, as also of a few *Cysticerci* like *C. Tæniæ cucumerinæ* and *C. cyclopis*, and yet again of *Bothriocephalus*, &c. In all these the modifications in the course of the passage into the final state are in all probability restricted to an elongation and segmentation of the "body" which is attached behind the proper "head." But if the supposition be correct, that the former is nothing but the body of the embryo which has formed a "frame for the head," then the embryonic body has in these cases its share in the formation of the jointed worm much in the same way as in the Ligulidæ. The growth and jointing take place, indeed, sometimes in the definitive, sometimes in the intermediate host; but the difference which is here expressed cannot be ranked as a very weighty one, especially since we find numerous examples, especially among the Nematodes, where the parasites do not by any means always reach the same degree of development within their various primary hosts.

In the other Cestodes, *i.e.*, in all those which are in their larval state provided with a differentiated caudal bladder, whether "dropsical" or parenchymatous, the metamorphosis into the tape-worm proper is less direct, for the growth and jointing of the body is always preceded by the loss of the bladder.

We owe our knowledge of these metamorphoses to the above quoted (p. 332) memoirs of Küchenmeister and v. Siebold (or Lewald).

By their experiments, which were mostly made with genuine bladder-worms, and especially with *Cysticercus pisiformis* of the rabbit, we know that the separation of the bladder begins very soon after the transference of the bladder-worms into their final host, and is complete when they have passed (in about five or six hours) from the stomach to the small intestine, where the now evaginated head becomes fixed by its attaching organs. As to the nature of the process there can be little doubt. The separation is an actual digestion which has naturally its first and greatest effect on the caudal bladder, since this presents so large a surface to the action of the digestive juices. This can take place even outside the living organism, as I have elsewhere shown,[1] for the process may be induced by an artificial digestion. For this purpose I used the fresh stomach of a dog, into which I transferred the bladder-worms, and then exposed it to the warm moisture of an incubating apparatus.

The experiment is not without interest, since it enables us to watch the worms in the full possession of their vitality. As a rule the bladder-worms appear as extremely sluggish creatures with hardly perceptible motion. But when the moist warmth acts upon them, one notices a lively peristalsis in the bladder, and a protrusion of the body, and can often observe the head pushed out, feeling in all directions, and may even notice how the suckers and the apicial rostellum extend themselves like tentacles, and then again retract.

FIG. 223.—Head of *Tænia solium* from the intestine of a rabbit, showing various phases of motion. (× 25.)

The same phenomena may be observed on the isolated bladder-worm heads, when one takes them from the intestine of a newly killed animal (Fig. 223). They persist until the loss of warmth puts a stop to the lively motions.

After the digestion of the bladder in the stomach of the animals under experiment, that is to say, after the lapse of about five hours, only the cylindrical body and the head are left. The latter is usually not stretched out until the worm passes to the small intestine; adhering to the posterior end of the body of the worm, one usually finds a few half-digested remains of the caudal bladder.

Hitherto it has been commonly believed that this body, after the loss of its adherent shreds, passed directly, by solidification and jointing, into the future tape-worm body.[2] In the first edition of this

[1] "Blasenbandwürmer," &c , p. 156.

[2] According to Küchenmeister ("Parasiten," 2d ed., pp. 72 and 96) this worm body. (= "Brutkapsel," Küch.) furnishes only the " primary terminal joint of the colony."

work I myself expressed this opinion, but have been convinced by repeated experiment that this structure disappears as completely as the caudal bladder. This indeed occurs some hours later, when the worm has reached the small intestine, but this is readily explained by the greater resistance offered by the more parenchymatous structures to the action of the digestive juice.

Thus, of the original worm only the head with its long narrow neck remains,[1] and produces by its metamorphosis the jointed tape-worm. And this is not the case only in the ordinary bladder-worms,

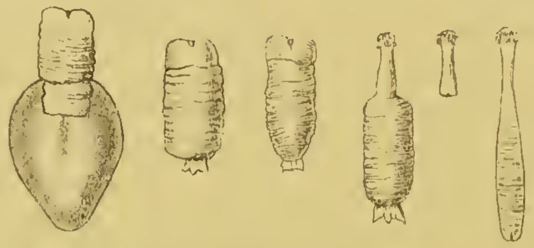


FIG. 224.—Metamorphosis of the bladder-worm of the rabbit into the young tape-worm. (× 4.)

but also, according to my observations, in *Cysticercus fasciolaris*, although in this case the appendage has even in the bladder-worm stage grown out into a long, jointed, tape-worm body (Fig. 202).

Posteriorly, where the neck passed into the appendage, there may at first persist a few traces of the former body of the worm, but these vanish within twenty-four hours after the transference of the bladders, and then only a small, almost scar-like, notch is left to recall the former state. The scar can be detected on the terminal joint of the chain till the latter is liberated. It leads into a small bladder-like cavity (Fig. 228), the porus terminalis, which receives the four longitudinal vessels. The cavity which formerly penetrated the head and neck has disappeared through the coalescence of the opposite surfaces, and thus sections already show the subsequent condition of the parenchymatous sheath. The musculature of the receptacle has not the slightest share in filling up the head.

In the Cysticercoids, whose anterior portion consists entirely of head and neck, the caudal bladder alone is lost. It is doubtful whether the same may be said of those forms whose caudal bladder is destitute of any histological differentiation. Judging from the analogy of the *Echinococcus*-heads, it is possible that the bladders may persist, as has been hinted at above, and pass directly by segmentation into the adult tape-worm.

[1] With this agree the results of Moniez, as stated in his essay on the history of the bladder-worm, which has just appeared.

The elongation and segmentation of the cervical portion[1] is as a rule perceptible after a very short time. In *Tænia serrata* I have usually been able to distinguish with the naked eye, within forty-eight hours of the feeding process, a chain of from twelve to eighteen joints. In other cases, however, not a trace of the segmentation was visible even after four days. Sometimes one finds, even in the second or third week, only a few straggling joints in a tape-worm perhaps a foot long.

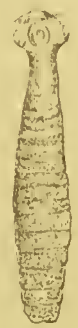


FIG. 225. — *Tænia serrata* twenty hours old, with incipient segmentation. (× 10.)

As to the ways and means by which the individual joints gradually grow and become sexually mature, we shall have much to say in our detailed survey. Here we shall only note that the youngest and smallest joints always lie next the head,[2] and only become mature after they have been pushed out to some distance from their point of origin.[3] On the other hand, the smallest, even microscopic, joints show essentially the subsequent musculature, though individual bands may be unequally developed. The main mass of parenchyma consists, of course, of distinctly nucleated cells, which multiply rapidly, and pass subsequently into the connective tissue ground-substance, or into the various generative organs. For the latter purpose, the cells group themselves in strands or masses, and either directly form the reproductive material, or, through the formation of an inner cavity, become epithelial (endothelial) structures, which occasionally acquire a more or less firm cuticular layer.

We have already seen some instances of the way in which the form and independence of the joints may vary, and the same manifold

[1] I speak purposely of the "segmentation of the neck," for the widely prevalent opinion that the joints arise through budding is strictly speaking incorrect. The joints are not produced by buds, that is to say, not by portions which are appended to the parts already present, and which develop without their participation ; they arise by the growth and modification of parts already present (the so-called "neck"), as has been shown above (p. 380) in the case of *Tetrarhynchus*, and as may be similarly, though less conspicuously, demonstrated in the case of *Tænia*.

[2] Here I ought perhaps to refer to Moniez's opinion, according to which (*Bull. sci. dep. du Nord*, p. 293, 1879) the head of the tape-worm represents not the anterior, but rather the posterior end of the body. Moniez regards the tape-worm as a simple animal, and denies the existence of an alternation of generations, and is able by means of the above theory to remove the difference between the tape-worms and the segmented worms, as regards the position of the buds, which, as is well known, are in the latter always before the anal segment.

[3] [The first formed joints are very commonly, though to a different extent in diverse species, sterile, and smaller than the later ones. Where they are numerous, as, *e.g.*, in *Tænia perfoliata*, the appearance of the young colony is so different from that of the older, that they have been regarded as different species. Thus, *Tænia plicata*, Auct., is only the young stage of *T. perfoliata* with a large number of sterile joints.—R. L.]

differences obtain in regard to their number. We know tape-worms with only three or four joints, and some with as many thousands, hence the period of a joint's development must also vary greatly. In the larger tape-worms, several months pass before the first joint is liberated, while in other cases only a few days are required.

At first sight it looks as though the head remained almost unchanged, and was only of importance in the formation of the chain in so far as it furnished, as it were, the raw material for the latter; but this view is not confirmed by closer observation and comparison,[1] for not only does it grow for a while in its Tænioid state, but its hooks often become larger and thicker by the deposition of new chitinous matter on the roots and on the base. The changes are indeed usually but slightly marked, so that they escape observation in the majority of cases. *Tænia echinococcus* is, however, an exception, since the differences in the size and shape of the hooks at different stages are so striking that for a while they caused perplexity in the study of the nature and life-history of the form in question. Among the Bothriadæ also we know of a form (*Echineibothrium*) which does not complete the development of its armature till it reaches the tape-worm stage.

In all cases the metamorphosis of the bladder-worm into the tape-worm takes place only after the transference of the former into the intestine of a suitable host. In its original abode the bladder-worm remains what it was. It grows to a certain size, and may live on perhaps for years, but a further development is impossible in this environment.

As to the age which bladder-worms as such may attain, we have as yet but few results, and what we have relate only to the forms found in vertebrates. The *Echinococcus* is credited with the longest life. We know of individuals who have suffered from this parasite for thirty years and more. A deduction from this as to the other bladder-worms is, however, illegitimate, for in *Echinococcus* we have to do, not with single individuals, as in the *Cysticerci*, but with generations, of which the oldest have long since perished, while the young forms are

[1] This would be still more evident, if it be true, as Mégnin has just asserted (*Comptes rendus*, t. xc., p. 715, 1880), that after a longer or shorter existence the head loses its hooks and suckers, and is finally so thoroughly absorbed that only the chain of joints remains. In this acephalous state the latter persists till the youngest joint is ripe, and the life of the tape-worm thus comes to an end. This has indeed been observed by Mégnin only in a few species (*Tænia infundibuliformis* of the fowl and *Tænia lanceolata* of the goose), but he does not hesitate to infer that the same may be true of the other species, though the length of life is often very long. [In this connection we may not unfitly recall the curious *Idiogenes otidis* of Krabbe (*Vid. Meddel. nat. Foren. Kjöbenhavn*, p. 122, 1867), one of the Tæniadæ, which is known to be headless and possessed of a very peculiar anterior segment.—R. L.]

ever forming themselves anew. It is probable that the ordinary bladder-worms do not usually persist in their hosts more than a few years.

In the examination of measly animals one sometimes finds specimens with protruded head, which have a very turbid, withered appearance, and exhibit no signs of life. When the surrounding cyst is unmodified, one may plausibly conclude that the parasites have died a natural death. As a rule, however, the cause of death must be sought in the pathological state and modification of the surrounding connective-tissue capsule. In such cases the secretory activity of the capsule has probably been in some way altered. Indeed one sometimes finds not only cysts whose under surface has an abnormal character—perhaps strongly injected or covered with small proliferations—but also others which have a bloody or even purulent fluid next the worm.

When the worm dies, whether from internal or external causes, its body-parenchyma at once begins to get turbid, and its bladder-fluid to be absorbed. The latter is gradually thickened, and acquires an almost gummy character. Afterwards the worm undergoes the same changes as may be observed in foreign substances introduced into the body-cavity. As the body of the worm becomes more and more shrivelled up and deformed, the albuminoids become displaced by a fatty mass which fills the collapsed connective-tissue cyst, and is finally calcified by the deposition of lime salts in varying abundance. On closer examination one often finds inside such cysts the still unchanged tape-worm hooks, which most indisputably prove the origin and nature of the apparent pseudoplasms.

In some cases these changes undergone by the dead bladder-worm exhibit various, but little studied, divergences. Thus there is in the pathological collection at Giessen a *Cysticercus tenuicollis* whose caudal bladder—not the cyst, as one might sooner have expected—is calcified all over, and seems almost ossified, without the form being at all altered.

Having now discussed the development of the tape-worms in its most important modifications, let us cast a glance at their life-history. Five successive stages are to be noted: (1.) the six-hooked embryo; (2.) the bladder-worm or *Cysticercus;* (3.) the tape-worm head without joints (*Scolex*); (4.) the proper chain-like worm (*Strobila*); and (5.) finally, the isolated sexual animal or *Proglottis.* The life-history of the Cestodes is therefore much richer and more complicated than we usually find even among the lower animals.

On closer examination these five phases are reduced to three different forms,—the round embryo, the tape-worm head, and the

sexual segment. These three forms represent as many generations, and all three form together a life-cycle. We have already given reasons for regarding the two latter forms as individuals, and the claims of the six-hooked embryo will be doubted by no one who considers its history without bias. The sexual animal results by asexual reproduction from the tape-worm head, and remains for a period in union with it, forming the worm-chain or Strobila. In the same way the tape-worm head has its origin in the embryo. The manifold metamorphoses undergone by the latter do not in any way affect its individuality. The caudal bladder of the *Cystiecreus* is, like the homologous *Echinococcus*-bladder, a morphologically independent structure; it stands in the same relation to the tape-worm head as the latter to the sexual animal. Like the jointed tape-worm, the typical bladder-worm is morphologically not a single individual, but a colony, with joints at different stages of development.

Of the three different generations which are distinguishable in the Cestode life-cycle, only one—the Proglottis—is sexual. Both the others are preparatory, and have only the power of asexual reproduction.

The life-history of the Cestodes seems, therefore, to be an alternation, with two "nurse" forms—one a "nurse" in the proper sense of of the term, the *Scolex*, the other a "grand-nurse" (Grossamme), the six-hooked embryo.

We should, however, be doing violence to nature if we tried to apply this formula rigidly in all instances. For, besides the forms in which we can observe the three successive generations in sharp and distinct contrast, there are others in which these developmental stages have so little independence, and follow one another so gradually, that it is impossible for us any longer to credit them with distinct individuality. The structural variations, elsewhere spread over different generations, appear in these cases merely as developmental phases of the same individual: the alternation of generations is replaced by a metamorphosis.

We have in the course of our survey noted many of these cases,—some where it was impossible to distinguish nurse and grand-nurse as individualised structures, and others where nurse and sexual animal were bound up in one. The *Scolex*-forms may suffice for illustration of the former case, and *Archigetes* of the latter. Perhaps we should also regard the Ligulidæ as forms in which the three otherwise separate generations are condensed into one, so that we cannot speak of an alteration of generations.

In the light of the many surprising results of the study of animal development, these facts do not seem specially unique. We know how in the lower animals the "individual" has often only a restricted

independence, and is physiologically subordinated to the rank of an organ. We know also that between reproduction and growth no sharp definite boundary line can be drawn; that, in other words, the phases and phenomena which we are wont to denote as individuals and as reproduction, have a certain adaptive mutability, and have only gradually acquired their characteristic properties. And thus we must not be astonished when we find that conceptions, usually sufficient, are not universally applicable; that an alternation of generations may be condensed into a simple metamorphosis; and a metamorphosis may spread over several successive individuals so as to constitute an alternation of generations.

It is not the Cestodes alone which furnish us with examples of this sort; we find others, some of them still more striking, among other animals, such as the Cœlenterata, where the group of the Hydromedusæ, or jelly-fish, furnishes us with most convincing proofs of the correctness of our conception.

SYSTEMATIC ACCOUNT OF THE CESTODES.

Rudolphi, "Entozoorum s. verm. intest. hist. nat.," 1808-1810.
Fr. S. Leuckart, "Zoologische Bruchstücke," Heft i., 1819.
Dujardin, "Hist. nat. des Helminthes:" Paris, 1845.
Van Beneden, "Vers Cestoides," *Mém. Acad. Sci. Bruxelles*, t. xxv., 1851.

It is not only in regard to the life-history and development of the Cestodes that our knowledge has increased in scope and completeness; the same must be said of our knowledge of the different forms and their natural relationships.

Apart from the bladder-worms and certain more isolated species, such as *Ligula*, the older naturalists knew only a single genus of tape-worms, *Tænia*. It was, therefore, an important step when Rudolphi not only increased the number of the unsegmented tape-worms by the erection of different genera (*Caryophyllæus*, *Tricuspidaria*), but also separated a number of species from *Tænia* on the ground of the structure of the head (*foveis duabus* instead of *osculis quatuor suctoriis*), and formed them into a special genus, *Bothriocephalus*. Although Rudolphi himself, in his later writings, prepared the way for the further breaking up of this family, by establishing a group of *Rhynchobothrii* (*i.e.*, *Tetrarhynchi* grown into tape-worms), it remained for long with its original content. This persisted, indeed, until van Beneden made us acquainted with the manifold Cestode forms parasitic in rays and sharks, and was not only compelled by his extended knowledge to erect numerous new genera, but made, for the first time, an attempt towards a natural division of the group, which henceforth included also the bladder-worms.

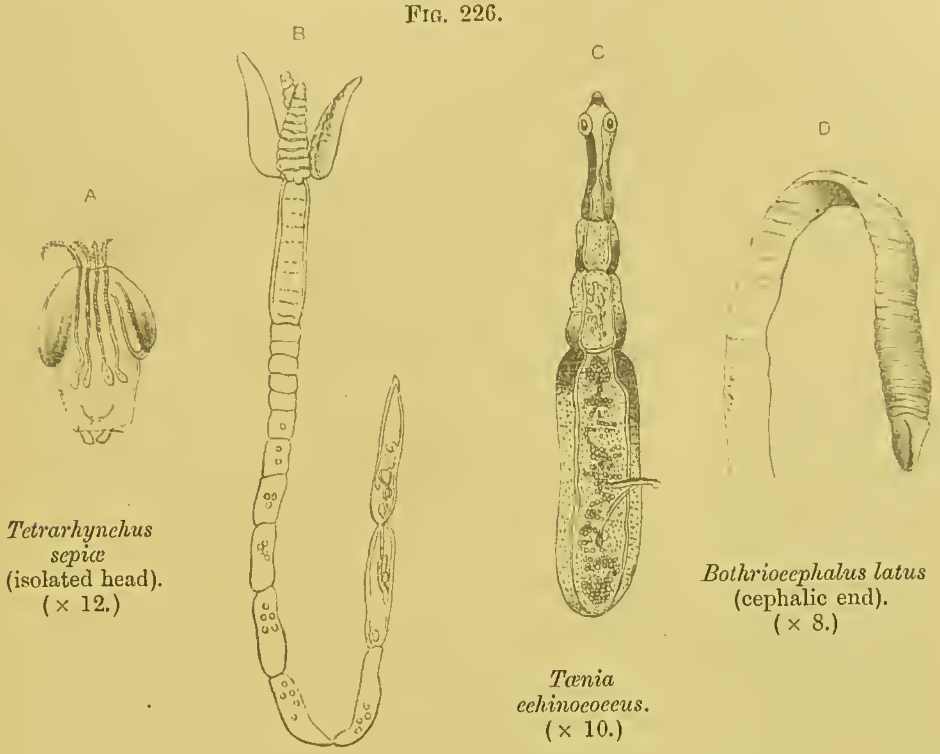
Van Beneden distinguished four families of tape-worms, distinguished according to the number and structure of their suckers: the *Tetraphylles, Diphylles, Pseudophylles* (= *Bothriocephali sensu stricto*), and *Aphylles* (*Téniens*). It seems doubtful whether the group Diphyllidia, which is only represented by a single genus, *Echineibothrium* (Fig. 226, *B*), should be retained; I should rather divide the Tetraphyllidia into *Rhynchobothria* and *Phyllobothria*, so that the Cestodes would then fall into the four groups—*Rhynchobothria* (*Tetrarhynchi Phyllobothria, Tæniadæ,* and *Bothriocephali* (or *Dibothria*).

The *Rhynchobothria* (Fig. 226, *A*) have a large head with four long proboscides and four large suckers, which often coalesce in pairs.

The *Phyllobothria* have four—rarely two—large, moveable, and often very complex suckers, sometimes furnished with spines anteriorly, and sometimes without armature.

The *Tæniadæ* are characterised by the want of a special uterine opening, and more especially by the possession of four simple suckers, between which on the apex there is usually one complete circle of hooks, but sometimes more.

FIG. 226.



Tetrarhynchus sepiæ (isolated head). (× 12.)

Echineibothrium minimum (after van Beneden). (× 8.)

Tænia echinococcus. (× 10.)

Bothriocephalus latus (cephalic end). (× 8.)

In the *Bothriocephalidæ* the attaching apparatus is reduced to two longitudinal grooves, which have only a slight mobility, and sometimes become so shallow that they can hardly be regarded as independent structures. Only in a few cases do we find hooks at the anterior end. The segmentation is often indistinct, and sometimes wholly disappears, so that the whole body forms one united mass.

Man is infested by various species of Cestodes belonging to the two families of the Tæniadæ and Bothriocephalidæ. The majority belong to the former of these families, which is indeed most widely distributed among terrestrial animals. The human Tænioid parasites in the adult stage are—*Tænia saginata* (*T. mediocanellata*), *T. solium*, *T. cucumerina*, *T. nana*, *T. flavomaculata*, and *T. madagascariensis*,[1] some of which,

[1] According to Heller ("Darmschmarotzer," in Ziemssen's "Handbuch d. spec. Pathol. u. Therapie," Bd. vii., 2, p. 560), there is in the Pathological Institute at Erlangen another still undetermined *Tænia*, which was voided by a child.

indeed—at least *T. cucumerina*—are only to be regarded as occasional visitors. They are found exclusively in the small intestine, which they share with two *Bothriocephali*—*B. latus* and *B. cordatus.*

But it is not only adult Cestodes which are found in man. He also harbours a number of Tænioid bladder-worms, viz., *Cysticercus cellulosæ* (of *T. solium*), *Cysticercus acanthotrias* (of *T. sp. ?*), *Cysticercus tenuicollis* (of *T. marginata*)—though this is not beyond doubt—and the *Echinococcus* (of *T. echinococcus*). Some of these grow to a very considerable size, and occasion manifold dangers, from which hardly any organ is exempt. Specially important, however, are the *Echinococcus, Cysticercus cellulosæ, Tænia saginata, T. solium,* and *Bothriocephalus latus.*

The following synopsis shows the systematic arrangement of the forms treated of in the present volume :—

Family TÆNIADÆ.

Genus Tænia.

Division I.—**Cystici.** (Cystic Tape-worms.)

Sub-genus *Cystotænia,* Leuckart.

1. *Tænia saginata,* Göze (*Tæniarhynchus,* Weinland) (p. 406).
2. *Tænia solium,* Rudolphi (*Cystotænia sensu stricto*) (p. 488).
3. *Tænia acanthotrias,* Weinland (p. 561).
4. *Tænia marginata,* Batsch (563).

Sub-genus *Echinococcifer,* Weinland.

5. *Tænia echinococcus,* v. Siebold (p. 586).

Division II.—**Cystoidei.** (Ordinary Tape-worms.)

Sub-genus *Hymenolepis,* Weinland.

6. *Tænia nana,* v. Siebold (p. 657).
7. *Tænia flavo-punctata,* Weinland (p. 661).

Sub-genus ——— ?

8. *Tænia madagascariensis,* Davaine (p. 663).

Sub-genus *Dipylidium,* Leuckart.

9. *Tænia cucumerina,* Rudolphi (p. 665).

Family BOTHRIOCEPHALIDÆ.

Genus *Bothriocephalus.*

1. *Bothriocephalus latus,* Bremser (p. 683).
2. *Bothriocephalus cristatus,* Davaine (p. 735).
3. *Bothriocephalus cordatus,* Leuckart (p. 736).
4. *Bothriocephalus liguloides,* Leuckart (p. 745).

FAMILY I., TÆNIADÆ.

The small pear-shaped or spherical head bears, at some distance from the apex, four roundish suckers, which are situated at tolerably equal distances from one another, and possess a powerful musculature of their own. Between the suckers there is usually, near the apex, a simple or manifold circle of claw-like hooks. To support and move the latter, there is a capsular muscular apparatus—the rostellum—which protrudes more or less from the crown of the head, sometimes even resembling a proboscis, which can also be retracted.

The proglottides are distinctly separated from one another; in their adult state they are usually longer than broad, and are almost always provided with marginal generative openings, sometimes confined to one side, sometimes alternating irregularly on both sides. In some cases also the joints have a pore on either side. The number of sexual joints varies greatly (from three up to three or four thousand); the length of the adult tape-worm is, therefore, also subject to much variation. The liberation of the proglottides takes place with great regularity, but somewhat late, after the embryos are almost fully formed. The uterus has no direct communication with the exterior, so that the eggs remain inside the proglottides, and are only set free when these are destroyed.

FIG. 227.—Head of *Tænia solium*. (× 35.)

The yolk-glands are but slightly developed. During development the embryos, while increasing continually in size, become surrounded with an often multiple envelope of more or less firmness. Since the transference of the eggs into the uterus is restricted to a comparatively short time, one finds them almost all at the same stage of development.

In the adult state the Tæniadæ live especially in terrestrial animals—mammals and birds—while the larval forms (bladder-worms, or *Cysticerci*) are found in very diverse higher and lower animals. They possess, with few exceptions, a well differentiated caudal bladder, but show manifold peculiarities as regards their proliferation. Sometimes they form distinct polycephalous colonies. Those occurring in the mammals usually attain a considerable size, which is largely due to the copious accumulation of watery fluid in the bladder.

Specially characteristic are the varied peculiarities exhibited by the organs of attachment. So distinctive are they, that one can, even with a hasty glance, recognise the Tæniadæ and distinguish their different species. This is of course true, especially of the forms armed with hooks, but even those with suckers only are readily recognised.

In details the armature varies exceedingly. The hooks which compose it have a conical form, and have their points turned backwards; but in size and number, shape and arrangement, they vary so much and so strikingly, that almost every one of the nearly two hundred species has its own characteristic appearance. Just to suggest the range of these variations, I may mention that the number varies from eight to several hundreds. Krabbe counted 360 in a *Tænia* from the emeu, and even 860 in a form found in the quail. Their size varies from 0·4 mm. (*T. crassicollis*) to 0·01 mm., and even less, so that sometimes the embryonic hooks may be larger than those of the adult. If the number be small, then the hooks stand usually in a single circle, but are as a rule in a double, or sometimes even in a triple or quintuple ring. In many cases, the double ring looks very like a single one, owing to the minuteness of the intervening space. The hooks of the second row alternate with those of the first, and are usually distinguished by smaller size and different shape. Sometimes the hooks of the posterior row differ in number from the others.

FIG. 228.—Longitudinal section of a young *Tænia serrata*, consisting almost entirely of head and neck. (× 60.)

The hooks are attached by a sort of root, which is sunk into the cuticle of the head. It is usually laterally compressed, and produced forwards and backwards into a more or less conspicuous process. The hinder is always turned towards the crown of the head, and is generally the longer, though in some species the reverse holds true. In the angle between the two root-processes, which of course belong to the same radius, the above-mentioned rostellum is fixed, so that the hooks are, in a certain sense, seated upon the latter.

This rostellum is the most important, if not the only motor apparatus which the hooks possess, special muscles attached to the root-processes being, as a rule, wanting in the *Tæniæ*. The rostellum has the form of a sometimes lenticular, sometimes oval or cylindrical bulb, of a more or less powerful muscular character, and able, according to its form and state of contraction, to exert pressure either on the posterior or

on the anterior root-process, in consequence of which the hooks are respectively retracted or erected.

The rostellum is in principle very like the proboscis of the *Echinorhynchi*, only that the latter has on the whole a more powerful development, and is able to exhibit much more effective movements. This resemblance is not, however, always equally evident, as a closer examination will show us.[1]

I regard as the simplest form of this rostellum that which is found in *Tænia cucumerina* of the dog and cat (= *T. elliptica*, Auct.). It consists of a closed sac, which, when quiescent, has an oval form, and is longitudinally embedded in the crown of the head in such a way that the anterior segment, which bears the hooks, protrudes like a boss ensheathed by the cuticle. The boundary of the sac is formed of a structureless membrane, which is possessed of considerable elasticity, and is firmly connected with the subjacent musculature. The latter is composed of two kinds of fibres—some circular, which surround the posterior two-thirds of the sac, and which lie, therefore, behind the hooks, and some longitudinal, which belong exclusively to the anterior portion, and run from the circular muscles, converging towards the apical surface of the sac. The interior of the sac is filled with a somewhat soft, clear, connective substance, which is penetrated by a network of fine fibres, and encloses numerous nucleated cells.

FIG. 229.—Rostellum of *Tænia cucumerina*. (× 140.)

These two groups of muscles are obviously to be regarded as antagonistic. By the contraction of the circular fibres, the posterior half of the rostellum is constricted, and instead of cylindrical it becomes club-shaped, owing to the accumulation of connective substance in the thereby distended anterior end. The hooks are forced to change their position on the now more strongly curved surface; if the pressure, as one would expect, be greater on the posterior root-processes, which are directed towards the apex, then the points of the hooks must move backwards and therefore sink in. When the circular muscles are again relaxed, the longitudinal fibres[2] empty the

[1] As to the structure of the rostellum, see, in addition to Leuckart ("Blasenbandwürmer," p. 63, note), also especially Nitsche, *Zeitschr. f. wiss. Zool.*, Bd. xxiii., p. 181, and Steudener, *Abhandl. naturf. Gesellsch.* Halle, Bd. xiii., p. 408, 1877. I must, however, note that I am not able entirely to agree with Nitsche's conclusions, especially in this, that I regard the "elastic cushion" of the cystic tape-worms as muscular, and as in reality forming the rostellum.

[2] In spite of their somewhat divergent insertion, these retractors plainly represent the

anterior end, and produce a uniform distribution of the connective substance, and by the re-assumption of the former cylindrical shape relieve the root-processes from their pressure. If the muscles act more vigorously, then the arched anterior end of the rostellum may even become more or less deeply depressed, so that any effect on the position of the hooks is removed.

With the movements of the hooks is usually associated a protrusion of the rostellum itself, which is, of course, accomplished by the surrounding muscular masses. Especially important are the longitudinal body-muscles, which can be traced into the head, and partly attach themselves directly to the outer surface of the rostellum. By these muscles, the latter can be retracted to a variable extent, so that the circular margin of the head becomes closed over it. The protrusion is effected by means of the transverse muscles which constrict the body, and in consequence drive what it encloses in the direction of least resistance. In many cases there are special muscular arrangements for the purpose, sometimes in the shape of well-developed protractors, which are stretched between the front of the head and the rostellum, sometimes as muscles investing the rostellum laterally and posteriorly, and developed in various ways. Thus, we find in the *Tænia undulata* of the thrush, &c., round the proper rostellum, a second muscular sac, which extends nearly to the circle of hooks, thus leaving the anterior end of the bulb free. By means of the longi-

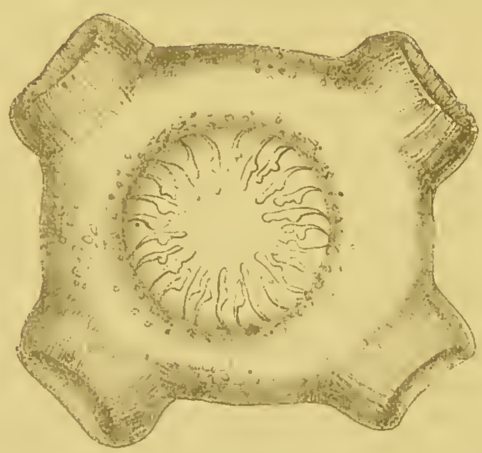


FIG. 230.—Rostellum of *Tænia undulata*, after Nitsche. (× 100.)

tudinal and circular fibres of its walls, it is able to act powerfully on the rostellum, and that all the more since the intermediate space

retractor muscles running inside the proboscis sheath of *Echinorhynchus* (see Vol. II.), which deserve all the more notice since the four proboscides of *Tetrarhynchus* show exactly the same arrangement of muscles.

is filled with the same clear connective substance which we have already observed inside the rostellum.

A similar arrangement is to be observed in the *Cystotæniæ* (Fig. 234), only that here the muscles both of the outer sac and of the rostellum are considerably thickened at the expense of the inner space. Rostellum and sac, therefore, appear as almost solid muscular masses, whose true nature is all the more readily overlooked, since, in their flattened character and external configuration, they differ from the above described extended proboscis-like apparatus. We shall afterwards return to their discussion.

Like the rostellum, the suckers of the Tæniadæ are organs which, by the development of a homogeneous boundary sheath, are sharply distinguished from the surrounding body-parenchyma, and therefore acquire a certain anatomical independence. All the four lie, of course, at the same height, in the equatorial line where the head is broadest, and are, in spite of their depth, usually entirely buried in the substance of the head, so that only their borders project. According to the height of these projections, the head appears more or less quadrangular. The corners represent in position the lateral borders of the body, and so far repeat even its flattened character, since the intervals separating the suckers are greatest where

FIG. 231.—Apical surface and circle of hooks in *Tænia solium*. (× 80.)

they correspond to the surfaces of the body. We need hardly mention that the suckers in the various species vary widely both in relative and absolute size. The strength of the musculature differs also widely, thus, of course, affecting the fixing power of the worms. The arrangement of the fibres, however, is on the whole uniform throughout, as was to be expected from the uniformity of the action performed.[1]

[1] [Quite recently the structure of the suckers in the Tæniadæ, as well as in other groups of animals, has been made the subject of a special treatise: Niemiec, "Recherches microscopiques sur les ventouses," *Rec. zool. suisse*, t. ii., p, i., 1885.—R. L.]

The main mass consists naturally of fibres, which increase and diminish the internal cavity. The former are by far the most numerous and powerful, and consist of radial fibres, which are usually united into bundles and are stretched between the two surfaces of the wall of the cup, and have their outer ends all directed towards the centre of the strongly curved interior cavity (Fig. 234). As in other situations, the fibres are embedded in a clear connective substance, which is on the whole much degenerated, but here and there exhibits distinct nucleated cells. The circular fibres counteract the radial, and lie in groups among the former, preserving on the whole, though with frequent deviations, an equatorial direction. On the border of the cup they are developed into a regular sphincter, which is capable of being greatly narrowed, and then protrudes almost like a diaphragm. At the same time, the radial fibres of the border are also variable, inasmuch as they gradually change their former angle of insertion (90°) for one extremely acute.

Besides these muscles, there is usually present on the convex outer surface a system of meridional fibres, which are much less strongly developed than the others, but in the species with powerful suckers sometimes form an exceedingly beautifully plexus. There are also many other modifications, especially in the superficial musculature, which have not yet obtained close attention.

FIG. 232.— Cephalic end of a *Tœnia cœnurus* with hexamerous symmetry. *A*, transverse section of a sexually mature joint. (× 25.)

Change in the position of the suckers is, of course, effected by those muscles which are attached to the elastic envelope. They are fibrous bands which are separated from the general body musculature, and mostly belong to the longitudinal system. Some of them run into direct attachment with the external wall of the suckers, while others bend from their former direction, and, crossing the fibres of the adjacent side, enter it at a greater or less angle. In connection with the quadruple number of the suckers, we have previously referred to the fact that the ventral and dorsal surfaces in the Cestodes have but a comparatively slight differentiation, and in the head especially are scarcely distinguishable. These conditions are seldom so pronounced in bilateral animals, but are characteristic of those animals which we are wont to oppose directly to them and to call Radiata.

It is not uninteresting in this connection to note that the head of the Tæniadæ sometimes exhibits a malformation which we not unfrequently find in radiate animals with tetramerous symmetry, viz., an increase of

radii to six. Such a head exhibits an increased number of hooks (in *T. cœnurus* I have counted thirty-two, instead of twenty-eight), and six suckers and longitudinal vessels, instead of the normal four. Usually they are approximated in pairs, of which three are present. The head, as a whole, has at the same time somewhat increased in size.

But in such cases it is not only the head which is abnormal; even the jointed body of the worm has had a corresponding share in the change. The neck shows, instead of ordinary flat shape, a triangular form, and this passes by the growth and further development of the proglottides into a structure which can hardly be otherwise described than that of a double formation, and which, in its extreme forms, is in principle entirely comparable with the double monsters which are sometimes to be observed in man and in other animals. The parts which, in the normal condition, are developed into the right and left halves of a single body, become in such a case the outer halves of two bodies which lie at an angle to one another, but have a single interior half in common. The size and independence varies widely in individual cases—perhaps in connection with the disposition of the superfluous suckers.

Even Bremser had noted these abnormalities as double monsters, and had observed the connection between them and the presence of six hooks.[1] Later observers (Küchenmeister and Leuckart) have been able to do little more than confirm Bremser's report, which has thus obtained general acceptance. Küchenmeister will not consent to regard them as abnormalities, but as a variety, since they are determined by what is really a "special law of development," and not "a capricious deviation in development."[2] This is, however, illegitimate, being founded on conceptions which have been long since rejected in Teratology. Besides, from our present standpoint, there is no fundamental distinction between abnormalities and varieties, and therefore the question as to the nature of these structures would be quite irrelevant if Küchenmeister had not also regarded the form with tetramerous symmetry as a variety equivalent to that with hexamerous. Quite apart from the fact that a species cannot possibly consist of mere varieties different from one another, to place the two forms on an equal platform is an unwarranted exaggeration, since the hexamerous forms occur as a very small minority, perhaps only in one case out of a hundred.

We find these six-rayed forms in many tape-worms, especially among the *Cystotæniæ*, which have indeed furnished us with

[1] "Lebende Würmer," &c., p. 107.

[2] "Parasiten," 2d ed., p. 145, note.

almost all the instances. We shall afterwards return to these structures, and will only now note that they have occasionally been described as distinct species, as, for example, the *Tænia* from the Cape of Good Hope distinguished by Küchenmeister, and the *Tænia lophosoma* of Cobbold.

Whether these malformations are hereditary, as Küchenmeister supposes, must remain undecided till it is settled experimentally. But what we know of the occurrence of six-rayed bladder-worms is only in favour of a spontaneous origin, since they are always found singly among normal specimens which probably originated from the same brood. In *Cœnurus* the six-rayed heads are found even on the same bladder as the four-rayed,[1] as one may conclude from the fact, that, after "feeding" I found in a dog one six-rayed (or triangular) tape-worm—but one only—among the numerous specimens with four suckers.[2]

Even the hooks sometimes undergo sundry malformations besides the variations in number above referred to. These concern both the root-like processes and the claws, and are sometimes so marked that, instead of the proper hooks, only more or less irregular chitinous knobs, in which one can at first glance hardly recognise the characteristic and beautiful head armature. In the cases I have seen these malformations mostly concern the whole circle of hooks, so that their conditions must be sought rather in the common place of attachment than in the individual papillæ. Even a total abortion of the circle of hooks has been observed.

The numerous abnormalities of the proglottides we shall have further opportunity of studying. They are abundant enough, especially in *Tænia saginata*, but may be for the most part reduced to a sometimes luxuriant, sometimes imperfect, or even wholly absorbed segmentation. Occasionally one meets with tape-worms in which a second segment is found laterally attached. The supernumerary segment is in such cases usually partly abortive, though the contrary also occurs. Moniez describes a case of *Tænia marginata* which forked in two places,[3]

[1] This fact contradicts Moniez's supposition (*Bull. Sci. dep. du Nord*, p. 202, 1878) that such a head might result from a twelve-hooked embryo, such as he had often observed (see p. 330).

[2] My experience of trianglar tape-worms is not exclusively limited to this one case, but also includes two other cases of *Tænia saginata*. One of these, viz., Küchenmeister's *T. capensis*, I have formerly described (First German edition of this work, Bd. i., p. 308).

[3] "Observations tératologiques chez les Ténias," *loc. cit.*, p. 201. I may also mention that Moniez has at different times observed that *T. expansa*, and once the *T. denticulata* found along with it, were infested with Psorospermiæ. What Moniez has so designated is not, however, in any way a Sporozoon (see p. 191), but a so-called *Micrococcus* (*Panhistophyton*), and therefore a fungus, similar perhaps to those which I once found in *Oxyuris* see Vol. II.), and which Bütschli has also found in free-living Nematodes. Moniez also reports finding his Psorospermiæ in *Echinorhynchus proteus*.

thus producing each time two chains running side by side, which were, however, so unequally developed that each supernumary chain looked like a short lateral branch. Recalling the familiar fact that lizards, after losing their tails, not unfrequently produce a double tail, it may perhaps be presumed that the doubling is in the above case also the result of an injury in which the chain had been lost up to the proliferating neck. Perhaps it may even happen, as is probably the case in the lizards just mentioned, that the terminal portion gets torn longitudinally, or in some other way irregularly injured.

In *Tænia cœnurus* I have observed a remarkable malformation which one may perhaps regard as a *situs inversus*. The last eight to ten joints of the chain exhibited perfectly normal sexual organs, but in inverted position, inasmuch as the organs which should lie posteriorly — namely, the female reproductive organs — were situated anteriorly. The connection of this terminal chain with the anterior entirely normal portion was effected by a short joint, with only testes and two peripheral knobs lying opposite one another, which, in spite of their resemblance to genital pores, had neither recognisable openings, nor cirrhi, nor vasa deferentia.

FIG. 233.—Supernumerary joint of *Tænia saginata* ($\times \frac{1}{2}$).

Also it not unfrequently happens that in a series of quite normal joints a segment is interpolated with only male organs. We have already noticed some other deviations in the formation of the sexual organs (p. 278).

Most zoologists include in the family Tæniadæ only a single genus —*Tænia*. This genus is, however, so rich in species—we know almost 250—and these exhibit such striking and deep-seated divergences in armature, sexual organs, form of the egg, and mode of development, that we seem fully justified in splitting up the genus into a number of smaller groups. This is not of course the place to enter specially into the systematic arrangement of the Tæniadæ, but we are bound to give a rational treatment to the differences between the various tape-worms infesting man, and that with reference to a natural grouping of the genus.

The Tæniadæ, then, we first divide into two groups (see p. 390), which differ especially in the nature of their development. The first group includes the cystic tape-worms, which are distinguished from the others by a great number of peculiarities, and exhibit developmental phases formerly distinguished as *Cystici*. Not that the bladder-worm stage, as

such, belongs exclusively to this group; on the contrary, the other Tæniadæ are also mostly bladder-worms in their youth, as has been formerly noted in discussing their development. But the bladder-worm stage of the latter represents a less perfect organization, not only on account of its smaller size, but especially on account of the less developed state of the embryonic caudal bladder. On these grounds, therefore, there is some reason for distinguishing them from the true *Cystici*, and we will in the meantime designate them "*Cysticercoidei*."

Group A.—*Cystic Tape-Worms* (*Cystici*).

Tschudi, "Blasenwürmer," Freiburg i. B., 1837.
Von Siebold, "Band- und Blasenwürmer:" Leipzig, 1854.
Leuckart, "Die Blasenwürmer und ihre Entwickelung:" Giessen, 1856.
Moniez, "Essai monogr. sur les Cystercerques," *Trav. instit. zool. Lille*, t. iii.: Paris, 1880.

These tape-worms are mostly of appreciable, and sometimes even of considerable size. The head is very rarely unarmed, but is always provided with a strongly muscular, lenticular, slightly projecting rostellum, and a double, in some cases even triple, circle of hooks, which decrease in size, and often change their form in the posterior rings. Besides the claw, one can always distinguish two strong root-processes, running one anteriorly,[1] *the other posteriorly, of which the latter is the longer, especially in the anterior row. The proglottides, when ripe, are of a longish oval form, and have a uterus whose longitudinal main stem runs up the middle line, and in course of time develops a number of more or less independent, generally much divided, lateral branches. The vagina runs from the middle of one side downwards in a curve to the end of the uterus, and there comes into connection with the common duct of the two hand-shaped ovaries, and of the yolk-gland lying behind these. The testes are numerous, and are diffused throughout the whole body. The generative openings are found in irregular alternation on the right and left sides. The cirrhus-pouch and seminal vesicle are of small size. On the eggs one finds round about the embryo a firm shell of a brown colour, and a more or less distinctly granular character, which is originally surrounded by a second clear and distinct envelope. The embryonic hooks are short and thin, and all the six are of uniform structure.*

In both stages they live exclusively, so far as we know, in the Mammalia; as tape-worms, especially in Carnivora; as bladder-worms, especially in Rodentia and Ruminantia.

[1] [The reader is reminded that these words refer to the hook itself, not to the whole *Tænia*.—W. E. H.]

In summing up these peculiarities we have referred to the structure of the rostellum. It consists, as we mentioned, of a lenticular bulb, which bears hooks, and effects their movement by its variable contractility. The projecting circular ridge of the rostellum is situated in the interspace between the root-processes, and brings these into contact with the adjacent surface in such a way that the longer so-called posterior processes lie on the anterior surface. The latter only requires to change its radius of curvature to be able to act by means of the processes on the position of the hooks. This change of form occurs all the more easily and readily, since not only is the musculature of the bulb specially strong, but the subjacent body-muscles come into special relation to the latter.

Our knowledge of these arrangements is specially due to the investigations of Nitsche,[1] which were indeed primarily concerned with *Tænia crassicollis*, but which, according to my observations, are also applicable to the other tape-worms, at least to *T. solium* (of which Nitsche was able to examine only one badly preserved specimen), *T. serrata*, and *T. cœnurus*. Nitsche was, however, mistaken in regarding the bulb, which is the true rostellum, as only an elastic cushion without proper contractility, and only able to change its form and position by means of the muscular apparatus which surrounds it as a shell. The error involved in this conception is sufficiently displayed when we compare Nitsche's "elastic cushion" with the rostellum previously described in the case of *T. undulata*, which only differs in this, that the bulb and sac are much less muscular than in our cystic tape-worms. To bring the structure of the latter into harmony with the typical form, we only require to suppose that the musculature has developed greatly at the expense of the interior space, otherwise filled with connective tissue, and has finally caused the cavity to disappear.

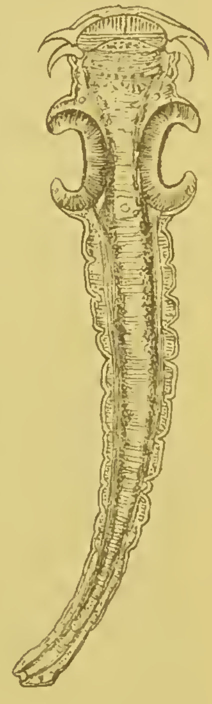


FIG. 234.—Longitudinal section of a young *Tænia serrata*, consisting only of head and neck. (× 60.)

Not much more remains to be said regarding the histological structure of the rostellum. Under a sharply defined porous and structureless external coat one finds a great number of fine fibres, which have a very regular course, and which fill up the whole mass of the bulb, with the exception of a few, mostly separated, connective-tissue cells. The arrangement of the fibres reminds one in many particulars of that previously described in regard to the sac-like rostellum of the

[1] *Zeitschr. f. wiss. Zool.*, Bd. xxiii., p. 183 *et seq.*, 1880.

Cysticercoids, but is more complicated, inasmuch as here we have not only longitudinal and circular muscles, but also a system of radial fibres which run from the middle point of the posterior surface diagonally to the side-wall of the bulb (Fig. 234). The latter is further ensheathed by a layer of circular muscles, which have been overlooked by Nitsche, while those running longitudinally are stretched straight between the two surfaces. In contraction these two surfaces would be equally approximated were not the anterior one, which is covered only by the skin, more moveable than the posterior, and therefore more obedient to the action of the muscles. In consequence of this, when the longitudinal and circular muscles are contracted at once, the bulb changes its quiescent form for that of a meniscus, which is open towards the front, so that the hooks seated on the border assume an almost vertical position. But besides the longitudinal muscles, the radial muscles also exert a special force on the anterior surface of the bulb, which arches forwards, and moves the hooks downwards in proportion as the diameter of the posterior half narrows, and as the middle of the posterior surface draws itself inwards in consequence of the funnel-shaped arrangement of the fibres.

The operation of these radial fibres is further aided by the muscular mass which lies behind the bulb, and which has been compared above to the outer sac of the rostellum in *Tænia undulata*. This comes into action at the same time and presses forward the posterior wall of the bulb, which it surrounds as with a shell. This muscular mass (see Fig. 234) consists of a whole series (six to nine) of discs laid down one over the other, all of a meniscoid shape and surrounded by a common border, which is partly attached to the bulb itself, partly to the subcuticula surrounding it, and is even connected by some of its fibres with the lower roots of the posterior hooks, or rather with the sacs in which they lie. The arrangement of the fibres is, as Nitsche has shown, peculiarly complicated, for they bend in a bow-shaped curve away from the periphery to the centre, and then out again to the periphery, crossing one another in their course through the series of layers. I cannot in any way grant a morphological independence to this muscular mass, especially since its fibres come into frequent connection with the surrounding musculature, and since posteriorly they pass quite continuously into the ordinary muscles of the body.

We have already noted that the young stages of the cystic tapeworms are characterised by the accumulation of a large quantity of a watery fluid inside an embryonic bladder, which is penetrated by numerous excretory vessels and muscular fibres. In *Echinococcus* the presence of the muscular fibres has been denied, but they are nevertheless present, though in small numbers, and feebly developed.

This is perhaps connected with the notable thickness and rigidity of the cuticle, which would hardly permit of vigorous contraction. The worm exhibits so many peculiarities, especially in the development of its head, that we are bound to regard it as the type of a special group of cystic worms. As we have mentioned above, the occurrence of a special brood-capsule for the budding heads is very characteristic, and perhaps also finds its explanation in the excessive thickness of the cuticle.

Nor can we avoid noticing that, in regard to the cystic tape-worms, an assertion has been lately made by Mégnin[1] which throws doubt on all we have been affirming as to the nature and development of these animals, and even of all the Cestodes. According to his assertion, the cystic tape-worms are in no wise independent forms, but represent merely the heteromorphic condition of hookless tape-worms. The latter, says Mégnin, are the true typical *Tæniæ*, which require for their development neither change of host, nor cystic stage, but rather result directly from the six-hooked embryos whenever these find from the first conditions entirely favourable for their development. In other cases the animals develop only circuitously through a Cysticercoid stage, and may, according to circumstances, become a cystic tape-worm, or return by metamorphosis to the typical form. Thus, when the *Echinococcus* of a herbivore is transferred to the intestine of a carnivore, it becomes *Tænia echinococcus*, but it is developed into *T. perfoliata* whenever the head, as sometimes happens, reaches the digestive canal by perforation of the intestinal wall of the host. In the same way *Cysticercus pisiformis* develops in the dog to *Tænia serrata ;* but in the rabbit itself may become *Tænia pectinata.* (!)

The two species here named are the only ones which Mégnin specially discusses, although he is of opinion that every hookless *Tænia* has its representative armed form. For any proof of this statement one looks in vain. Our author has neither demonstrated the asserted relationship by experiment, nor made it probable by the existence of intermediate types. He has apparently no conception of the extent of the positive observations on the development and structure of the Cestodes, which are quite enough in themselves to disprove the conclusions which he has tried to establish on merely subjective grounds and analogies.[2]

[1] *Comptes rendus*, t. lxxxviii., p. 88, and in detail, *Journ. anat. et physiol.*, t. xv., p. 225, 1879.

[2] The opinions and conclusions of Mégnin on the Cestodes have been decidedly rejected, not only by me (*Archiv f. Naturgesch.*, Jahrg. xliii., Bd. i., p. 199, 1877), but also by Moniez (*Bull. sci. dep. Nord.*, p. 233, 1880). The latter is, indeed, as we have mentioned (p. 280, note) so far in agreement with Mégnin, since, according to his opinion, a great many of the *Tæniæ* undergo a continuous development within the same host.

A. Cystic Tape-Worms in which the Head arises within the Embryonic Bladder.

Subgenus Cystotænia, Leuckart.

We regard the cystic tape-worms in this division as normal forms, and give them the first place in our consideration, not only because they include the majority of the species, but particularly because in their mode of development they closely follow the typical process of the other tape-worms. To justify our assertion we may refer to what we have already (p. 339 *et seq.*) said about the development of the bladder-worms. What we have said will suffice also as an introduction to these worms and their peculiarities, so far as they are revealed in the young stages. Apart from the nature of the bladder and its usually very lymphatic contents, the presence of the above described receptacle is especially deserving of attention. It forms, as is well known, a muscular pouch, which surrounds the rudimentary head with more or less independence, and also subsequently encloses most of the body of the worm which gradually originates between the head and the bladder.

By the continuous growth of the former the receptacle becomes ever larger with increasing age, but never loses its compact shape. In consequence of this the worm inside draws itself more tightly together[1] till the receptacle can contain it no longer, and then it is gradually protruded by the evagination of its basal portion. This occurs most constantly and most strikingly in the *Cysticercus fasciolaris* from the liver of mice and rats, where the worm protrudes sometimes a finger's length from the bladder, and becomes by solidification and segmentation so like an adult tape-worm, that it has even lately been erroneously described as such (Fig. 236).

FIG. 235.—*Cysticercus cellulosæ* with the head in the receptacle. (× 2.)

To the subgenus *Cystotænia* we refer not only the species with the ordinary single-headed bladder-worm (*Cysticercus*), but also the *Tænia cœnurus*, which, in its youthful state, is well known to be polycephalous. This proceeding is amply justified by the development and subsequent condition of the head. The resemblance between *Cœnurus* and *Echinococcus* is only superficial, and by no means war-

[1] The opacity caused by the twistings of the body of the worm within the receptacle aggravates the difficulty of investigation to such an extent that the earlier, and sometimes even the modern (as in Davaine's work), descriptions and illustrations of the parts of bladder *in situ* are with few exceptions useless.

rants the union of the two species, though this has been frequently proposed by certain helminthologists.[1]

The number of species of tape-worm belonging to this group is, as far as we yet know, at most a dozen and a half. Of course we are as yet hardly acquainted with any but European species, and these but imperfectly, so that in course of time the number will probably be much increased.[2] With the exception of the *Tænia solium* e *Cyst. cellulosæ* and the *T. saginata* e *Cyst. bovis*, they are all found in Carnivora; in the cat, *T. crassicollis* e *Cyst. fasciolari*; in the dog, *T. serrata* e *Cyst. pisiformi*, *T. marginata* e *Cyst. tenuicolli*, *T. Krabbei* e *Cyst. tarandi*, *T. cœnurus* e *Cœnuro cerebrali*; in the fox, *T. crassiceps* e *Cyst. longicolli*,[3] *T. polyacantha* e *Cyst. sp.*; in the polecat, *T. intermedia*, *T. tenuicollis* e *Cyst. talpæ*, &c.

FIG. 236.—*Cysticercus fasciolaris* (nat. size).

The size of tape-worm body differs widely in the individual species, but is on the whole very considerable. The hooks also are always large and strong, except in a few species, such as the small *T. tenuicollis*, and indeed few other *Tæniæ* can equal these forms in this respect. The anterior root of the smaller hooks is broadened at the end and notched like an inverted heart.

In spite of much structural resemblance, the different species are not hard to distinguish from one another. It is true that one of our most famous helminthologists—v. Siebold—affirmed the opposite only a few decades ago, and declared emphatically that the *Tænia solium* of man was identical with the above-mentioned tape-worms of the dog, and also with *T. crassiceps* and *T. intermedia*. This has, however, been sufficiently disproved by Küchenmeister and by myself. Even if we regard the differences in size and habit as irrelevant in spite of their constancy, and due, as v. Siebold would have it, to the differences in the hosts inhabited, there are yet other weighty and distinctive

[1] Zeder unites these two to form the genus *Polycephalus*.

[2] In the liver of *Arctomys Ludoviciana* I observed just lately the *Cysticercus* of a hitherto unknown *Tænia*, with twenty-four extremely small hooks. Moniez has also enriched our knowledge of the bladder-worms by the discovery of a new species, *Cysticercus Krabbei*. It lives in the muscles of the reindeer, and is developed in the dog to a segmented chain (*loc. cit.*, p. 44).

[3] The doubt which Moniez casts (*loc. cit.*, p. 69) on the relationship between *Cysticercus longicollis* and *T. crassiceps* is quite gratuitous. I have associated the two forms not only because of the hooks, but because I have produced the *Tænia* in question from the *Cysticercus*. It is impossible to confuse the latter with the *Cysticercus talpæ* (which, though hookless, according to Rudolphi, is in reality provided with small hooks), although both species occur both in the mole and in the field-mouse, and although the former also has sometimes been designated *Cysticercus talpæ*. It is equally impossible to regard *Cysticercus longicollis* with Dujardin as a young *Cysticercus fasciolaris*.

peculiarities. This is above all true of the hooks, whose form, size, and number, though variable to a certain extent, are so characteristic of the different species, that on them alone one can, after some practice, establish a diagnosis. Not less distinctive are the differences in the anatomical structure, especially of the generative organs, and in the development, as we shall afterwards see, in the case of the forms which specially interest us. But granted that it were possible to explain all the differences between *Cysticercus cellulosæ* and *C. tenuicollis* or *Cœnurus*, or those between *Tænia solium* and *T. marginata* or *T. cœnurus*, on the theory of the variability of species—a theory which might with equal justice be considered as overturning all systematic zoology—yet one fact alone is enough to forbid the identification of the two forms. This fact is the result of experiment. The attempt to give a sheep staggers with eggs of *T. solium* or *T. serrata* yields no result, but after administering the ripe proglottides of *T. cœnurus*, we are not only sure of the result, but can predict the date of the appearance of the first symptoms with almost mathematical precision. By the oft-repeated experiments of Haubner, Baillet, myself, and others, it has been indisputably shown that certain bladder-worms always result from certain eggs, and pass into definite tape-worm forms. Besides, when one occasionally finds all the three tape-worms of the dog in the same intestine without any loss of their characteristic peculiarities, one can hardly persist in regarding them as mere varieties, owing their special form directly to the circumstances of their life.

a. *Cystic Tape-worms without Circlet of Hooks.*

(Tæniarhynchus, Weinland.)

Tænia saginata, Göze.

(Tænia solium, Auct. p. p., Tænia lata, Auct. p. p., Tænia dentata, Batsch, Tænia mediocanellata, Küchenmeister.)

Göze, "Eingeweidewürmer, &c.," p. 269 (*T. cucurbitina, grandis, saginata*).
Küchenmeister, "Cestoden, &c.," p. 107, tab. ii., 1853 (*T. mediocanellata*).
Idem, "Parasiten," first German edition, p. 88; second edition, p. 140 (*T. mediocanellata*).
Leuckart, "Parasiten," first German edition, Bd. i., p. 258 (*T. mediocanellata*).

This is the largest of the human Tæniæ, *and when extended measures* 7 *or* 8 *metres, but in its contracted state is only about* 4 *metres long; it is composed of from* 1200 *to* 1300 *segments, of which more than three-fourths belong to the anterior half of the body. But it is not its length alone that characterises this worm; it is also of unusual breadth and thickness, and is provided with segments which are remarkable for their*

size and firm appearance. Especially characteristic is the breadth of the middle segments, which amounts to 12 *or* 14 *mm. The neck seldom measures less than* 1 *to* 1·5 *mm. Since the length of the segments increases comparatively slowly, the great majority are broader (sometimes three or four times broader) than they are long; only the ripe proglottides containing embryos are (even in their contracted condition) of the well-known melon-seed shape. The large hookless head* (1·5 *to* 2 *mm.) has a flattened crown, with a pit-like hollow in the middle, and has four large and very powerful suckers, which, however, usually project only slightly, and are frequently surrounded by a black, more or less broad, pigmented border. In the mature proglottides the same pigment is often found in the vagina, vas deferens, and testes. The complete development of the germ-producing organs takes place at about the* 600*th segment, while the embryos only attain maturity* 360 *or* 400 *joints further on. The number of the so-called "ripe" segments may be estimated at from* 150 *to* 200. *The eggs have a thick shell, with a border of little rods. They are generally markedly oval, and almost always provided with the primordial yolk-skin. The uterus which encloses them is characterised by the large number (twenty to thirty) of its lateral branches, which run out close beside each other, and exhibit many dichotomous divisions. The greatly projecting porus genitalis lies in the ripe proglottides on the lateral margin, at a perceptible distance behind the middle.*

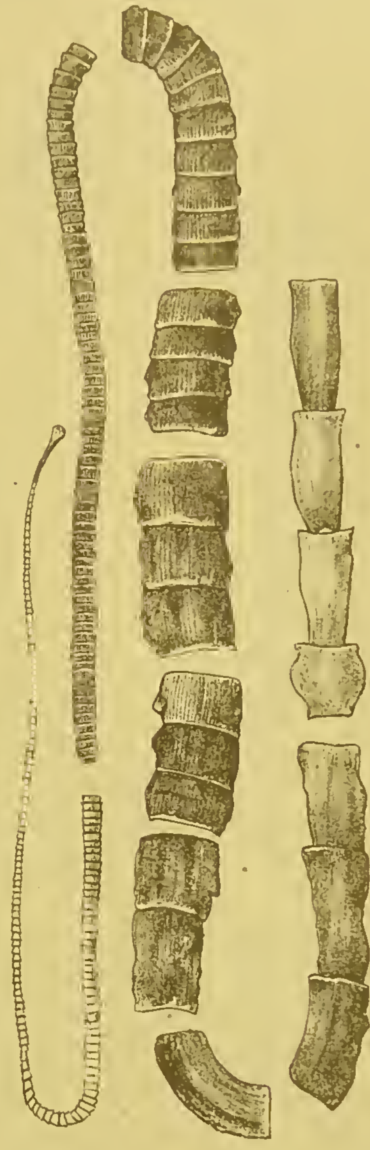


FIG. 237.—*Tænia saginata* (natural size).

If, as often happens, the joints have been spontaneously liberated, they are generally found without eggs and shrivelled up, but still of considerable size and thickness. Before the evacuation of the eggs they generally measure from 18 *to* 20 *mm. in length and from* 5 *to* 7 *mm. in breadth. The new formation and growth of segments take place so quickly, that about eight, or even more, proglottides are separated daily, even when, as is the rule, only a single worm is present.*

The bladder-worm generally inhabits singly the muscles of the ox, but is occasionally found in the internal organs. It contains only a small quantity of fluid, is of a roundish form, and hardly ever attains the size of 1 *cm.*

FIG. 238.

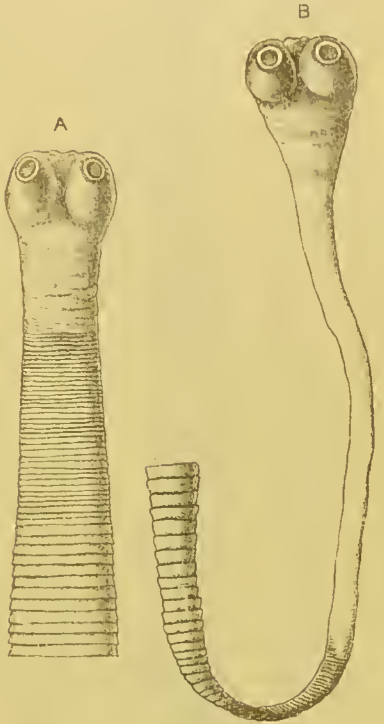


FIG. 239.

FIG. 238. — Head of *Tænia saginata* in contracted (*A*) and extended condition (*B*). (× 8.)
FIG. 239.—Ripe segment of *T. saginata.* (× 2.)

Historical Development of our knowledge of Tænia saginata *and the related Forms.*

We give *Tænia saginata* (*T. mediocanellata,* Küchenmeister) the first place in our description, partly because it is the only cystic tape-worm with unarmed head which occurs in man, and partly also from historic reasons; for, in opposition to the widely spread belief that the so-called *Tænia mediocanellata* was only discovered a few decades ago, a critical analysis of the existing information regarding the human tape-worms shows it to be the very species that has been longest known. For not only does the oldest complete picture of a human *Tænia* (that of Andry) unmistakeably represent *Tænia saginata,* but it is further quite indubitable that the *ἑλμίνθες πλατεῖαι,* and also the identical *ταινίαι* (or *κηρίαι*) of the Greeks—the *Lumbrici lati* and *Tæniæ* of the translators and commentators—refer especially to this species, and by no means to the *T. solium* of Rudolphi.

The descriptions of the ancients, it is true, do not supply any direct foundation for specific diagnosis. They are so unsatisfactory that in their time they did not even suffice to establish the animal nature of

the tape-worm. Even in the sixth and seventh centuries after Christ, Aëtius and Paulus Æginecta explained the tape-worm as a metamorphic product of the intestinal mucous membrane,[1] and in later authors one frequently meets with similar views. But there are not wanting positive proofs of our statements. First I would note that *Tænia saginata* is much more frequent in the countries round the Mediterranean, and especially in the East, than *T. solium*, which belongs more to the north of Europe. So, too, the statement of Hippocrates, that the tape-worm patient very often evacuates "quali quid cucumeris semen" (*οἷον σικύου σπέρμα*)—that is to say, that he voids in portions the ripe joints of the worm, or proglottides—describes a phenomenon which is much more frequent and much more striking in the case of *Tænia saginata* than of *Tænia solium*.

I will not, however, assert that it was exclusively *Tænia saginata* that was known to the Greek physicians. I can the less do this, since *T. solium* is by no means absent from the East, as is decidedly proved by the fact that the bladder-worm of the pig, from which it is descended, has been known there from antiquity. The only question is, what particular form it was with which the physicians of antiquity and of later times were most familiar, and to which their statements mostly refer? And that form is, as we have said, decidedly *T. saginata*. When *T. solium* occasionally occurred, there would seem to the older physicians all the less reason to mention it specially, and to distinguish it from the larger and more frequent, or at least more striking forms, since it is by no means very markedly different from *T. saginata*.

The Arabian physicians and their immediate successors must also have made their investigations mainly on *Tænia saginata*. This may be inferred not only from the geographical distribution of the two worms, but because, like Hippocrates, they regarded the exit of the so-called *Vermes cucurbitini* (Chabb-al-Kar'i) as proof of the presence of the tape-worm, and were even many of them of the opinion that the latter only originated subsequently from the former by the formation of a chain.

At any rate, the exit of the tape-worms, which seemed to the ancients so characteristic, excluded the supposition that their *Lumbricus latus* is the same as the present *Bothriocephalus latus*, which, instead of separate joints, usually gives them off only in numbers. And since the latter is almost absent from the countries in the Mediterranean basin, and if found in the south and south-east of Europe, is usually confined to Switzerland, and the districts in its immediate

[1] "Lumbricus latus transmutatio, ut ita dicam, est membranæ intestinis intrinsecus agnatæ in corpus quoddam animatum."—Aëtius, "Medicina tetrabiblos" iii., serm i., cap. xl., de lumbrico lato.

neighbourhood, it is very probable that it was quite unknown to the earliest physicians and naturalists. Certainly it did not enter into the minds of the first observers of *Bothriocephalus*—Thaddæus Dunus, in Locarno (1592), and Gaspard Wolphius in Zürich—to identify their worm[1] with the tape-worm of the ancients; although, after all, that proves nothing more than that the specific knowledge of the parasites was at that time extremely meagre and superficial. If they had had opportunity to compare their worm with the genuine *Tænia*, the difference between the two parasites would not have escaped their notice any more than it escaped that of the clinical physician, Felix Plater of Basle, who, in his famous "Opus praxeos medicæ" (1602), mentions them for the first time as two different human tape-worms. Plater's description is so expressive of the characteristics of this worm, and of the then prevailing views, that I cannot refrain from quoting it here. "Per podicem," says Plater,[2] "corpora . . raro ejiciuntur diversorum generum, e quibus unum fasciam quandam refert membraneam, intestinorum tenuium substantiæ similem, eorum longitudinem adæquantem, minime tamen, uti illa, cavam, sed digitum transversum latam, quam latum Lumbricum appellant, rectius Tæniam intestinorum, siquidem cum Lumbrico nullam habeat similitudinem, nec uti Lumbricus vivat aut loco moveatur, sed tamdiu, donec nunc integrum, magno impetu aut terrore patientis existimantis intestina omnia sic procedere, vel abruptum elabatur. In qua fascia plerumque lineæ nigræ transversæ, spatio digiti ab invicem distantes, per totam ipsius longitudinem, et ad formam vertebrarum in intervallis illis extuberantes apparent. . . . Alias vero aliter formata ejusmodi tænia longissima, veluti ex portionibus multis cohærentibus et quæ ab invicem abscedere possunt constare videtur, quas portiones, quum cucurbitæ semina quadrata nonnihil referant, cucurbitinum vermem vocant. Qualis rarius integer, sed plerumque in plura frusta divisus rejicitur; qua singula privatos vermes esse, cucurbitinos dictos, crediderunt, licet tantum fasciæ illius abrupta sint particula."

A century passed without Plater's statements receiving any important addition or correction. The two species of tape-worm which he established were pretty generally accepted, and were usually called the "species prima et secunda Plateri," but our knowledge of them was hardly at all advanced till Andry published his investigations.[3] Like

[1] That it was a *Bothriocephalus* that these physicians observed, can of course only be inferred, but with some probability, from their statements. Thaddæus, for example, ("Miscell. med.," cap. v.) describes the worm as "squamosus, instar serpentis, nisi rectius geniculatus," which could scarcely apply to *Tæniæ*.

[2] *Loc. cit.*, t. ii., "De anim. excretion."

[3] "De la génération des vers dans le corps de l'homme" p. 51 *et seq.*: Amsterdam, 1701 (Reprint).

Plater, he also speaks of two species of the genus *Tænia*—" L'un, qui retient le nom du genre et qui s'appelle proprement *Tænia*, lequel n'a point du mouvement ni de tête formée; et l'autre, qui se nomme *Solium*, à parce qu'il est toujours seul de son éspèce dans les corps, oû il se trouve, et qui a du mouvement et une tête ronde fort bien formée, faite comme un poircau."

This is not the first time that we meet with the name *Solium*. Even earlier observers used it, the earliest, so far as is known, being Arnoldus de Villanova, who, in 1300, reports of a *Lumbricus*, "qui aliquando emittitur longior uno vel duobus brachiis, qui *Solium* sive *Cingulum* dicitur." Villanova had, therefore, found the name somewhere else. Its origin is uncertain, for the derivation from *solus* suggested by Andry is grammatically incorrect (on account of the *i*), and is as obviously made to suit the case as is also the derivation from *solium*, a throne—a word which suggests the solitary occurrence of the tape-worm (*Tænia saginata*), a fact of which we find a hint even in Hippocrates. The hook-bearing *T. solium* often occurs in groups.

In order to ascertain so far as possible the etymology of this strange appellation, I sought to interest my honoured friend and colleague Dr. Krehl, Professor of the Oriental Languages at Leipzig, in the question, and, to my great joy, have received from him the following explanation:—

"It is impossible," writes Krehl, "to derive the word *Solium* from the classic languages, and we are further directed towards the Oriental tongues by the fact that both in Arnoldus, who translated several works of Avicenna, and in his predecessors, a knowledge of them may be assumed. One naturally thinks first of Arabic; but none of the words by which the Arabs designated the tape-worm—for example *dûd* (worms), or *chabb-al-kar'i* (properly gourd-seed) agrees in sound with the word *Solium*.

"But as the Jews in the East and in Spain frequently busied themselves with the practice of medicine, or, more generally, with medical studies, Hebrew might be referred to; but with its *kôkcjânîn* or *kirsa* or *dûré* (? perhaps *dûdé*), it supplies nothing that might serve as an explanation of the word *Solium*. Under these circumstances I should like to offer as an explanation the certainly somewhat remote Syriac word for the tape-worm, namely, *schuschl-é* (properly "chains"), which is sufficiently attested by Bar Bahlûl (see Payne-Smith, "Thesaurus linguæ Syriacæ," i., 317, infr. s. v. *Askârîdes*), and by Ferrari ("Nomenclator Syriacus," p. 651).

"Medical science had reached a high development in Syria, and the Arabians doubtless first received from the Syrians an exact know-

ledge of the writings of the Greek physicians, and of the natural sciences. In this way the word would come to be used with its special meaning[1] by the Arabians, and through them by the French or Spanish authors of the Middle Ages. The phonetic transition from the original *schuschl-ê* (*ê* is only the plural termination) to *sol-ium* might be thus explained. Among the Arabians it would be changed into *susl* or *sosl*, and among the romance authors it would lose the second *s*, first in pronunciation, and then in writing, just as the disappearance of the *s* before the consonant can be proved in *même* (for *mesme*), *île* (for *isle*), *maître* (for *maistre*), &c. Sylvius says in his "Isagoge"—"*S* ante *t* et alias quasdam consonantes in media dictione (that is to say, in the middle consonant) raro ad plenum, sed tantum tenuiter sonamus et pronunciando vel elidimus vel obscuramus."

We shall now, however, turn from this etymological excursus, which has given us a thoroughly satisfactory explanation of a formerly almost meaningless appellation.

The above-mentioned statements of Andry are all the more important in connection with our subject, since they are accompanied by drawings and descriptions which leave not the slightest doubt regarding the nature of the *Tænia* or of the *Solium*. The "*Tænia*" turns out to be the present *Bothriocephalus*, with its uterine-coils, which were regarded as vertebræ (hence *Tænia* à épine), and the *Solium*" (*T.* sans épine) turns to be a large-jointed *Tænia;* not, however, the *Tænia solium* of later and modern helminthologists, but quite undeniably, as has already been mentioned, Küchenmeister's *Tænia mediocanellata*, with its firm joints and large black head[2] (somewhat too large in the picture). As to the idea that the four suckers were eyes, and that the uterine coils were vertebræ, we will pardon its *naiveté*, and by no means judge it so harshly as other investigators have sometimes done. The designation, "Ver solitaire," which Andry uses for his *Solium*, also suits *Tænia saginata*, and was but little objected to until men acquired a more accurate knowledge of *Tænia solium*, Rud., which often occurs in numbers.

Andry was, however, not the only investigator of that time who described the modern *Tænia saginata* as *Solium*, as is shown, for instance, by the pictures in Vallisnieri's treatise, "De vermium humani corporis." These figures undoubtedly represent the characteristic peculiarities of the former worm.

[1] It may be pointed out in this connection that even at the present day the tape-worm (*Tænia saginata*) is extremely prevalent in Syria.—See *Mém. acad. Méd. Paris*, p. 998, 1877.

[2] "Ce ver a la tête noire, plate, un peu arrondi, où sont quatre ouvertures, deux d'un côté et deux autres au côté opposé," *loc. cit.* This shows how incorrect is the assertion of Küchenmeister ("Parasiten," 2d ed., p. 141, note), that Andry saw no head in his *Tænia*.

But an exact and detailed description of the worm was still lacking. Only after the course of half a century was this want apparently supplied by a treatise of the famous Genevan natural philosopher Bonnet, "Sur le ver nommé en latin Tænia, en français Solitaire."[1]

The description given by Bonnet in this work of the head of the particular tape-worm, which he observed, agrees in all essential points with that of Andry. It is true that he only succeeded in finding it once with certainty, but in this case it appeared distinctly, just as Andry described it, as a small black knob, which was placed on a thin neck, and consisted chiefly of four plugs arranged in pairs and with only one terminal opening. The surface (apex) lying between the suctorial plugs, which, in the other tape-worms (as especially shown by Tyson in the four from the cat)[2] is provided with circles of hooks, in this case exhibited nothing but a shallow depression (*un enfoncement*).

But in spite of this conformity there was a great and striking difference between the two descriptions; for, from the structure of their joints, Bonnet's tape-worms belonged, not to the first but to the second species of Andry and Plater, or, in other words, they were not *Tæniæ*, but *Bothriocephali*.

Since Bonnet made his worm the subject of thorough investigation, and supplied the first really correct figure of it, at Geneva, where *Bothriocephalus* was very frequent, and where he had abundant opportunity of observing the parasite, it was easy to suppose that the head structure, first observed by Andry in the tape-worms, occurred in the "*Tænia*" (= *Bothriocephalus*, Rud.) and also in the "*Solium*" (the modern *Tænia saginata*)— assuming of course that the description of Andry was based on no oversight or error.

And indeed this supposition long obtained favour, and was not refuted until thirty-seven years later. A mistake had, indeed, been made—not, however, by Andry but by Bonnet. The worm whose head Bonnet described really represents a *Tænia saginata* (*Solium* of Andry), but the joints mentioned in connection with it originated from the modern *Bothriocephalus*.

Possibly the confusion arose from the circumstance that Bonnet,

[1] *Mém. de Mathematique et de Physique prés. à l'Acad. roy. Paris*, t. i., p. 495, 1750.

[2] With the exception of the statements of Tyson and Andry, any account found in ancient literature of the head-formation of the tape-worms is based on gross errors and fantastic misrepresentations, which may here be omitted. I refer any one who is interested in these to Tyson, "Lumbricus latus," *Phil. Trans.*, vol. xii., No. 146, p. 124, 1683, and to the compilation of Werner, "Vermium intest. br. exposit." tab. iv. : Lipsiæ, 1782. Even in the year 1762 Linné also flatly denies the existence of a head in the tape-worms ("Amœnitates Acad.," tab. ii., p. 66).

who had no opportunity of observing any other tape-worm than *Bothriocephalus*, and who believed that there was no other species in Geneva, had, when examining his *Tænia saginata*, only found a comparatively short chain of joints at his disposal, and the shortness of the anterior joints, which is so characteristic of this species, would all the more easily lead him astray, since he was inclined to base his specific distinctions principally upon the form of the joints, as may be seen from the fact that he named the modern *Bothriocephalus* (regarded by him as the *Lumbricus latus* of the ancients) " *Tænia* à anneaux courts," in contradistinction to *Tænia*, which he calls " *Tænia* à anneaux longs."

Although Bonnet himself recognised his mistake,[1] and exposed the delusion under which he had been labouring, by discovering the real head of his *Tænia lata* (*Bothriocephalus*), and demonstrating its wholly different structure, yet the false idea which he originated has been of most fatal influence in the history of *Tænia saginata*.

Bonnet's second work was less circulated, and the corrections were almost completely overlooked, and thus it happened that a worm called *Tænia lata* was known in helminthological literature until the time of Bremser (1819), who appreciated[2] Bonnet's later observations, and also recognised a species of Rudolphi's genus *Bothriocephalus* in Bonnet's worm. This so-called *Tænia lata* was said to be characterised by short joints, a median generative opening and coiled uterus (*à corps en manière de fleurs*), associated with a hookless head with four suctorial pits—a species, indeed, which does not occur at all in nature.[3]

Nor was it only a few or the more inexperienced who adhered to this error, but the greatest helminthologists of the time, headed by Pallas,[4] and including Göze,[5] Bloch,[6] and Rudolphi.[7] None of them had any hesitation in recognising *Tænia lata* as a fully justified species, without, however, being able in any way to confirm Bonnet's statements on the ground of their own investigations.

[1] "Nouvelles recherches sur la structure du Tænia," *Observat. sur la Physique, &c.*, p. 243, Paris, 1777.

[2] "Lebende Würmer," &c., p. 92.

[3] That the real *Tænia saginata* is sometimes designated by the name *Tænia lata*, instead of this fictitious animal, is shown by the fact that in the Giessen Zoological Museum, lately incorporated with v. Sömmering's collection of Helminths, there was a *T. saginata*, to which this name was affixed, while the *Tæniæ* (with hooks) were correctly named *T. solium*.

[4] "Bemerkungen über die Bandwürmer in Menschen und Thieren," *Neue nordische Beiträge*, i., p. 64, 1781.

[5] "Versuch einer Naturgesh.," &c., p. 298, 1782.

[6] "Abhandlung von der Erzeugung der Eingeweidewürmer," p. 17 : Berlin, 1782.

[7] "Entozoor. hist. natur.," vol. ii., p. 70, 1810.

Besides this *Tænia lata*, however, there figured among the human tape-worms a second species with short joints and median openings. This form was first advanced by Linné as *Tænia vulgaris*,[1] and was said to be distinguished from *Tænia lata* by its less broad body, and by its exhibiting two openings, one behind another, on the more extended joints, while *Tænia lata* had only one. Pallas, who, notwithstanding his knowledge of Bonnet's second treatise, firmly believed that *Tænia lata* was provided with four suctorial pits, thought that this *T. vulgaris* alone was furnished with the *Bothriocephalus*-head, and expressed the doubt whether what Bonnet had described as "a somewhat inflated delicate point, cleft longitudinally, but without papillæ or circlet of hooks," was really the head, and whether it might not be simply "the snapped end of the chain." Rudolphi, however, recognised neither this second short-jointed species, nor *T. tenella*, another form distinguished by Pallas, but classed them both with *T. lata*—a proceeding which was afterwards followed by the majority of investigators, and especially by Bremser.

These short-jointed human tape-worms with median pores were thus contrasted with the long-jointed forms, with laterally situated "osculum," which from this time were, after the example of Linné, generally (and always in our century) called *Tænia solium*. Pallas indeed departed from this rule by exchanging Linné's name for that of *T. cucurbitina*, a name which seemed in some measure justified, since he (Pallas) comprehended under it not only the long-jointed human tape-worms, but, further, the related forms in dogs and cats, which we now rightly regard as separate species. Among other characters, they were all credited with a cephalic armature, as had had meanwhile been repeatedly demonstrated by Tyson on the apex of tape-worms infesting mammals.

Linné had, moreover, already noted the circumstance that *Tænia solium* did not always exhibit exactly the same appearance in man. After having described the typical form (*Tænia saginata*), with references to Andry, Vallisnieri, and others, he continues[2] as follows:—"In hominibus sæpius hic ipse vermis maxime planus, macilentus et fere membranaceus ejicitur, instar vittæ, quod ex eo forte est, quum raro nisi mortuus ex homine expulsus obtineatur, et sic mortuus spiritu vini committitur, ut fibras suas ab irritatione spiritus contrahere nequeat, quemadmodum fit in vivo verme spiritui indito." It is further added that specimens in this condition somewhat resemble *Tænia vulgaris*.

The same fact was also noted by several of the later investigators,

[1] "Amœnitates academicæ," vol. ii., p. 69 : Holmiæ, 1762.

[2] *Loc. cit.*, p. 69.

but these differed from Linné, in so far as they did not ascribe the difference in the appearance and nature of the worms to any subsequent modification, but regarded it as original and present from the first. Thus Pallas[1] informs us that when *Tænia cucurbitina* occurs in dogs and wolves, it is often, in spite of perfect similarity in the form and proportions of the joints, considerably smaller than in man. And in regard to its occurrence in man, he adds, " that from reasons which do not seem exactly to harmonise with the apparent constitution of the host, and which are difficult to explain, it is sometimes delicate, thin, and slender, and at other times very large, thick, and as it were fattened," as he is able to prove " by remarkable examples " which he had expelled " from a thin and sickly girl between her twelfth and fifteenth year." In the largest and ripest joints, he says that the difference is sometimes in the proportion of one to three, for in the smaller animals the length and breadth of these joints is hardly four lines by two, while in the larger ones it is more than eight by five. If several tape-worms be voided, they are usually of about the same size and of similar form and joints, for he knows no instance of several " species " having been observed together in the same man.

The foregoing descriptions, and the reference to Andry, thus enable us to recognise in these large and thick worms our *Tænia saginata*, while the smaller and thinner ones are the present *T. solium*, which, except in the suggestions of Linné above-mentioned, is here distinctly described for the first time.

Göze declares himself still more definitely, and divides *Tænia cucurbitina*—which is here, however, exclusively confined to the human tape-worms—into two groups.[2] The former of these is " the familiar large one, with long, thick, flattened joints," and is named by him *Tænia cucurbitina grandis saginata;* while the latter, " which seems to be a variety of it, but continues to be the same under all circumstances," is designated *T. cucurbitina plana pellucida.* It is true that the heads are said to be provided in both groups with a circlet of hooks, but from the description and drawing it is evident that this supposition is based upon a mistake, for the first familiar form (Göze recommends Andry's figure, except the head, as pretty good) is evidently the unarmed *T. solium* of the older investigators. The second form, although less common elsewhere, is, according to Göze, the most frequent of the two around the Hartz.

Batsch agrees with this idea of Göze,[3] except that under the name *T. cucurbitina*—which he prefers to the " quite unsuitable " name *T.*

[1] *Loc. cit.*, p. 47.
[2] *Loc. cit.*, p. 278.
[3] " Naturgeschichte der Bandwurmgattung," p. 121 : Halle, 1786.

solium—he mentions, after Pallas' example, besides the "large and strong" and the "flat, delicate, and transparent" varieties, a third one, namely, "the cucumber tape-worm of the dog" (*T. serrata*, Rud.), which "ought not to be omitted, if the other two are explained as mere varieties." The differences between these forms, and especially between the first two, are, he tells us, very constant, and noticeable even in the formation of the branch-like division of the ovary, "although he will not venture to define them." He adds, further, that they have no connection with the constitution of their host, but that it rather appears as though the degree of frequency of both varieties were determined by the locality.

Later helminthologists have devoted less attention to the foregoing varieties of form, partly indeed because (being for the most part North Germans, especially Rudolphi) they lived and collected in districts where they mainly came across only one form. Their *Tænia solium* is pre-eminently the hook-bearing species still designated by this name. It is true that the great variability in the size and nature of the joints was sometimes noted, but it was not perceived that these divergences always occurred only in certain individuals, and characterised particular "genera" or "varieties," which we are now accustomed to regard as distinct species.

But of course the less this circumstance was noted, the more surprising did it seem that reports multiplied, according to which the head of the human *Tænia* was sometimes destitute of the circlet of hooks. It gradually began to appear as though there were, as Batsch had already conjectured, districts, or even whole stretches of country, in which *Tænia solium* was never, or only very seldom, found with an armed head.

Thus Bremser, the famous Viennese helminthologist, reports in his great work[1] that, in opposition to the general descriptions and figures of *Tænia solium*, he had sought in vain for the circlet of hooks, and that, in spite of the most minute examination of a great number of tape-worms (in Vienna), he had only seen it in a head sent by Rudolphi from Berlin. A worm with a hook-bearing head was afterwards sent to him from the general hospital. If Bremser had paid attention to the fact that the unarmed worm which he had observed also differed from the armed one in size and structure of the joints (all of his drawings very closely represent *Tænia saginata*), the explanation of the lack of hooks might perhaps have been sought in another direction than in the supposition (adopted by other investigators, and especially by my uncle, F. S. Leuckart, and Mehlis) that the tape-worm lost its armature with age, as a man loses his hair.

[1] "Lebende Würmer im lebenden Menschen," p. 100.

Neither did Wawruch ever succeed in finding an example with an armature of hooks[1] among the very numerous tape-worms expelled under his treatment in Vienna. It is also known that the south of Würtemberg, which lies in the basin of the Danube, furnishes almost exclusively the unarmed *Tænia* (Weishaar), while the districts drained by the Neckar yield, with but few exceptions, the armed species (Seeger)[2] In Java, Schmidtmüller[3] always found only the unarmed tape-worm, although, during the sixteen years of his residence there, he had opportunity to observe great numbers of them in the negro soldiers. From their description, they are undoubtedly *Tæniæ*, but the worms had, nevertheless, such an unusual appearance, and especially such broad joints, that Schmidtmüller was tempted to regard them as a special species of the genus *Bothriocephalus* (*B. tropicus*). The "broad tape-worms" (*Tænia lata*) observed by Tutschek in Tumale (Africa) were probably the same worms.

But now that we have become convinced that, with the special structure of the head of the human *Tæniæ*, there is also always associated a characteristic structure of the joints; in other words, that the *Tænia solium* of the helminthologists (and of Linné) comprehends two distinct species—one of them unarmed, with broad and thick joints, and the other armed, and with slender and thin joints. All these statements and observations find a simple and natural reconciliation. If only the true relation of these long familiar differences had been sooner understood, science would have been spared many serious errors, for even those which we have already mentioned do not by any means exhaust the whole number.

The reader will remember that Linné described by the name of *Tænia vulgaris* a form of the modern genus *Bothriocephalus*, which was distinguished from *Tænia lata* (*Bothriocephalus latus*) by the fact that there are two medially situated genital pores. Werner transferred the same name to a tape-worm, of which he met with four specimens in only one case out of about fifty,[4] and which resembled the Linnean species in so far as its joints were also provided with two pores. Although these pores were situated on the margins, and although, from the structure of its joints and head, the worm was decidedly a *Tænia*, and not a *Bothriocephalus*, Werner thought he could identify it with Linné's form.

Batsch, who recognised the impossibility of such an association, proposed the name *T. dentata* for Werner's worm.[5] He referred it to

[1] "Praktische Monographie der Bandwurmkrankheit," p. 34: Vienna, 1841.
[2] "Die Bandwürmer," p. 62: Stuttgart, 1852.
[3] *Hannoverische Annalen*, Bd. vii., p. 602, 1847.
[4] "Verm. intest. br. expositio:" Lipsiæ, 1782.
[5] *Loc. cit.*, p. 185; also Gmelin, "Syst. nat.," Edit. xiii.

the unarmed species, since in his description Werner said—"The existence of a circlet of hooks could not have been overlooked if it had been present with any distinctness." Instead of it, a median papilla is mentioned, lying between the suctorial cups, which recalled those of *T. solium*, except that they were larger, and visible even to the naked eye. In length, general appearance, and form of the joints these specimens closely resembled the common tape-worm of man, and particularly the broad form (*T. saginata*), but there was a striking difference between them in the doubling of the marginal pores.

But since two opposite peripheral openings sometimes occur in the common human *Tæniæ*, especially in *T. saginata*, and since such joints, like other similar malformations, often repeat themselves several times in the same worm, the supposition of Rudolphi that Werner's worm belongs to the so-called *T. solium* seems very probable.[1] Joints with two lateral sexual openings are, however, rare in the cystic tape-worms, while Werner credits the whole chain with double openings. It is just possible that the reports in question are due to the observer having erroneously generalised the peculiarities noted, which had never been previously observed. It strikes one as strange that a worm such as Werner describes should have never been rediscovered during the lapse of a century. A Saxon physician, Nicolai, did indeed describe a *Tænia dentata*,[2] but this worm, about which Nicolai said only that it "belonged to the rare species *Tænia dentata*"—thus identifying it, according to Batsch's nomenclature, with Werner's *T. vulgaris*—has only a single generative opening like the ordinary tape-worms. It is, indeed, nothing (as the accompanying description proves) but the common *T. saginata*, with its unarmed head and characteristic body-form.

In this *Tænia dentata* we find then, for the first time, a well characterised[3] second species of large-jointed *Tænia* infesting man—a species which is expressly designated as such, and as different from the ordinary *Tænia solium*. This difference holds true, however,[4] only in regard to "the flat transparent form" (our modern *T. solium*),

[1] "Entoz. hist. nat.," vol. ii., p. 76.

[2] *Neue Zeitschr. f. Natur- und Heilkunde*, Bd. i., p. 464 : Dresden and Leipzig, 1830.

[3] Nicolai diagnoses his species as follows :—"Tænia capite inermi acuminato sessili, articulis dilatatis brevioribus, marginis utriusque lateris medio elatiore, alterius osculato, majoribus transverse striatis, emarginatis."

[4] Nicolai was, indeed, quite unaware of this fact, and we can therefore understand his report when he says that the host of the *Tænia dentata*, shortly before expelling the latter, voided also "a piece of *Tænia solium* with unusually large joints, and about six inches long"—a piece which was obviously only the terminal portion of the subsequently voided worm.

for the common form with thick broad joints—the *Tænia solium* of the ancients—is as truly identical with this *Tænia dentata* as with the *Bothriocephalus tropicus* of Schmidtmüller.

Neither Nicolai nor Schmidtmüller was able to make out a good case for the specific distinctness of his worm. Their reports were but little noticed, and for the most part, indeed, entirely overlooked, so that the worms they had observed were, as before, referred to *T. solium* if they were alluded to at all.

This was the state of matters till, in 1852, Küchenmeister again advanced the opinion that besides *Tænia solium* there was another large-jointed species to be distinguished in man.[1] Both were, he said, well marked by distinctive and constant characters, partly in shape, partly in the structure of the head and of the uterus. Only one, the *Tænia solium,* is provided with hooks; the other, which is also the larger and broader, is unarmed.

If Küchenmeister had been better acquainted with the literature of Helminthology, and had consulted it more carefully, he would very soon have learned that his discovery was not so new as he supposed, but was rather only a confirmation and extension of observations which would have been long since fully settled if the observers had had a more rich and complete material to work upon. He would also have learned that the species described by him as new, and named *T. mediocanellata,* was nothing but the true *T. solium*[2]—the "familiar" tape-worm of the old helminthologists, the *T. grandis saginata* of Göze. This fact is not in the least altered by the circumstance that later zoologists have, in opposition to the common use of the term, come to refer the designation *Solium* to the flat transparent form (*T. plana pellucida* of Göze) first clearly defined by Linné. This is mainly due to the influence of Rudolphi, who, in Greifswald and Berlin, was able to procure only the latter form,[3] and was thus misled into the supposition that the long-jointed tape-worms of man belonged one and all to the same species.

Strictly speaking, then, Küchenmeister's *T. mediocanellata* should be called *T. solium*; but it would thus be necessary to find a new

[1] See especially, "Ueber die Cestoden im Allgemeinen und die des Menschen insbesondere," p. 85 *et seq.*, Zittau, 1853, and "Parasiten," Bd. i., p. 82, Leipzig, 1855. The third species mentioned in the latter passage—"the *Tænia* from the Cape of Good Hope"—has been withdrawn since I recognised it as merely a malformation.

[2] The *Tænia lata* mentioned by Küchenmeister can scarcely be referred to *T. mediocanellata.* It is, as we have shown, merely our modern *Bothriocephalus*, erroneously credited with the head of *T. saginata.*

[3] That Rudolphi had also seen the true *Tænia solium* (*T. saginata*), may be inferred from his record of two specimens which were, on account of their size, ranked beside the *T. vulgaris* of Werner, "Entoz. hist. nat.," t. ii., p. 76.

designation for the armed species, which has been generally known by the latter name in modern zoology. One might perhaps call it *Tænia pellucida*, following Göze's diagnosis. But by this change of name the confusion in the nomenclature of the tape-worms, which is already great enough, would only be increased. I feel myself, therefore, constrained along with Küchenmeister, in the interests of scientific intelligibility, to uphold the name of *Tænia solium* for the armed form.

It is thus the unarmed form which has to receive another name. Küchenmeister has, as we have seen, chosen for it the designation *Tænia mediocanellata*, which has since been frequently adopted. He confesses, however, himself that the choice is "not a very happy one," since it suggests the erroneous opinion which he at first upheld, that the uterine stems of the joints were united together into a common longitudinal canal. It must also be noted that Küchenmeister's *T. mediocanellata* had previously received, as we have seen, many other names. Thus, besides such names as *Tænia lata* (= *T. inermis*, Brera) and *Bothriocephalus tropicus*, which we may leave out of account since they rest on false presuppositions, it has been called *T. grandis saginata* by Göze, and *T. dentata* by Nicolai. It is surely not only justifiable, but really demanded, by the rules of zoological nomenclature, that the thoroughly unsuitable designation "*mediocanellata*" should be replaced by Göze's very appropriate name "*saginata*," as I proposed some years ago in my reports on the progress of the natural history of the lower animals.[1] Since this name has, in the meantime, been generally accepted — *e.g.*, in Claus' "Zoology" and Moniez's "Monograph,"—and has even obtained currency in medical writings through Lewin and Heller, and since Küchenmeister has himself declared that he was prepared to accept any name more suitable than his own, I have no scruple in using the name *Tænia saginata*.

Though Küchenmeister's investigations on the *Tæniæ* have now been rewarded by the appreciation they deserve, it ought to be mentioned that his newly described—and, as it appeared, newly discovered —"*T. mediocanellata*" was not at first recognised on all hands. A few investigators declared themselves distinctly in favour of ranking it as a distinct species, and sought to corroborate their opinion by investigation and experiment. Of these were such men as the elder van Beneden and A. Schmidt in Frankfort.[2] Others, on the contrary, remained neutral, or cast doubts upon the constant association of the characters upon which Küchenmeister relied, or would at most regard

[1] *Archiv f. Naturgesch.*, Jahrg. xxxiii., Bd. ii., p. 284, 1867.
[2] See the first German edition of this work, Bd. i., p. 238.

T. mediocanellata as a variety of the ordinary *T. solium*. Thus, Weinland, among others, reports that in an American tape-worm, which in size and structure of the head was exactly like Küchenmeister's species, he found precisely the same form of uterus as in *T. solium.*[1] He regards *T. mediocanellata* only as a common tape-worm, which has by chance, or perhaps in consequence of a sudden wrench, lost its rostellum with the hooks, and had therefore, by continuous use, gradually increased the size and strength of its suckers, the only remaining organs of attachment. The large size and thickness of the worm are consistent with such a supposition, since it is quite plausible that these forms, presenting a large surface to be affected by the pressure of the intestinal contents and the contraction of the intestinal wall, should therefore be most exposed to the danger of losing their circlet of hooks; and the same factors which determine the large size of the body, may possibly also be the causes of the abundant branching of the uterus, for that represents after all only the space-requirement of a great mass of eggs.

All these suppositions and hypotheses were, however, dismissed when I succeeded, some years after Küchenmeister (1861), in rearing the young form of *Tænia saginata*,[2] and establishing that the worm in question differs in its development from *Tænia solium* in a way as characteristic as it is striking. While the latter, as we first knew from Küchenmeister, is in its youth the familiar bladder-worm of the pig (*Cysticercus cellulosæ*), the young *T. saginata* is found not in the pig, but in the ox, as a hitherto unknown muscle bladder-worm, which is from the first destitute of hooks and of a rostellum, and is otherwise very different, especially in the size and structure of the rudimentary head.

By this demonstration, the question as to the nature and independence of *Tænia saginata* has been settled. To-day it is universally recognised as a species distinct from *Tænia solium*,—a species, moreover, which has a much wider distribution than the latter, indeed occurring wherever the ox is a domestic animal, and where its flesh is used as food. We find it in all countries, both in Temperate and Torrid Zones, and know that in districts where it is the custom to eat raw or almost raw flesh, as in Abyssinia, almost every one suffers from it from their earliest years. *Tænia solium* stands in the same relation to the pig as *T. saginata* to the ox, but is less common, since the breeding of swine is not so general as that of the ox, especially in hot countries.

1 "Essay on the Tape-worms of Man," p. 40: also, *Med. Correspondenzblatt des würtemb. ärztl. Vereins*, p. 31, 1859.

2 *Göttingen Nachrichten*, Nos. 1 and 2, 1862.

Growth and Structure of Tænia saginata.

Sommer "Ueber den Bau und Entwickelung der Geschlechtsorgane der Tænia mediocanellata," *Zeitschr. f. wiss. Zool.*, Bd. xxiv., p. 499, 1874.

The designation "*grandis saginata*," which Göze has given to this species, in contrast to the one which we now call *Tænia solium* (his "*plana pellucida*"), gives at once an idea of the characteristic size and appearance of the worm. It is natural, then, that the characters expressed by these words should be first used for specific diagnosis.

We must not forget, however, that these peculiarities are not always equally conspicuous. We find specimens, for instance, which, though perhaps of the normal length, have by no means the characteristic appearance, being far thinner and almost transparent, so that they might be readily referred to *Tænia solium*, were it not for the absence of hooks on the head, and the frequent ramification of the uterus.

As a rule the physician has not in his diagnosis to deal with the whole worm, but only with the isolated proglottides. The identification of the latter is a matter of great importance, since the *Tænia saginata* is very different from *T. solium*, both in its pathological and therapeutic aspects. For the latter involves much greater danger to the patient, for reasons which will presently appear, and is therefore to be removed as expeditiously as possible, while *T. saginata* admits of a more temporising mode of treatment, which is the more fortunate since the worm in question, though hookless, has a considerable power of resistance, and is only to be dislodged by very powerful and energetic means.

FIG. 240.—Isolated proglottides of *Tænia saginata* (nat. size).

The Proglottides.—It is of some aid in diagnosis to note that the proglottides of *T. saginata* are by no means so exclusively expelled in the stools as those of *T. solium*; in great part, indeed, they leave the host spontaneously, which is very rarely the case with the latter.

This power is due to the strong development of their musculature, which ensures a considerable mobility. This muscular development is shared of course by the whole body, and contributes not a little to the thick and fat character which we have already repeatedly emphasised as one of the characteristics of *T. saginata.* Even after leaving the intestine the proglottides retain for a while their mobility, and creep about in a definite direction till the continued lowering of temperature brings them to a stand-still. In lukewarm water their movements can be followed for hours. They move just like independent organisms, and were indeed formerly regarded as such (*Vermes cucumerini*). In the warmth of the bed they often creep over the whole body, especially if the skin be somewhat damp. The proglottides which Pallas detected on the wall, more than a yard above a patient's bed, were probably those of *T. saginata*, and not those of the less muscular *T. solium.*

Although it is always only the last and oldest joints which become separated from the chain and wander outwards, they are by no means always the largest. This is due to the fact that they generally lose a more or less considerable portion of their contents just when the separation commences, and are indeed occasionally liberated almost destitute of their eggs. As a rule, it is at the anterior border of the joints that the eggs escape, which is explained by the circumstance that it is at this point that the uterus, with its longitudinal canal and lateral branches, is most closely approximated to the surface, and is therefore most easily ruptured by the pressure of the contracting muscles. While the joint creeps about, the eggs are sometimes seen issuing in a stream from this point.

The decrease in size which ensues in consequence of the expulsion of the eggs, expresses itself in a diminution of the transverse diameter, which is sometimes (Fig. 237) contracted to less than 4 mm., and occasionally so much that the proglottides look quite cylindrical. Empty joints of this rounded form have been repeatedly sent to me as "thread-worms," although the nature of their body-parenchyma, and the constant distinctness of the lateral ridges, made their true nature at once obvious to the expert[1].

So long as the animals retain their mobility, one can observe a perpetual change of form; they are at one time stretched out and nearly cylindrical, and again they are contracted into a club or flask-like form, till finally they become short, flattened, broad, quadrangular bodies, still possessing a quite appreciable thickness, and recognisable in form and character as tape-worm segments. Throughout these

[1] Even a helminthologist must be reproached with having confused these joints with Oxyuridæ; see Coulet, "Tractatus de Ascaridibus et Lumbrico lato:" Lugd. Bat., 1729.

varied changes it is the anterior end which is most affected. It is at one time pointed like a cone, at another it is spherical, and again it is flattened like a spatula, as is the cephalic end of certain Planarians. It resembles the latter also in going first as the animal creeps. The more truncated posterior end changes its form but slightly, and with its everted border, which formerly embraced the adherent joint like a cuff, forms a distinct sucker, by which the animal fixes itself during its creeping movements.[1] Elongation and contraction succeed one another so rapidly that in a minute the joint can cover a distance of several centimetres. By unequal distribution of the contractions over the two halves of the body, the direction of motion is not unfrequently turned to the one side or to the other.

Fig. 241.—Proglottides of *Tænia saginata* in motion (nat. size).

The outer surface of the body is frequently wrinkled longitudinally, and is of a dirty white colour. The rusty brown eggs can sometimes be seen shining through the thick envelope of the body.

The Structure of the Uterus, which, with its numerous lateral branches, is so characteristic of *T. saginata,* is best examined by treating the proglottides with acetic acid, or with caustic potash, and then holding them against the light, pressed between two glass plates.

In such preparations one observes first the median stem of the uterus as a wide, though not uniformly filled, longitudinal canal running up the middle of the joint. It extends forwards almost as far as the outer wall, while posteriorly it stops short of it at a

[1] This happens even in the segmented condition, according to an observation made by Göze on *T. crassicollis* (*loc. cit.*, p. 346), which may be quoted as showing the great mobility of these animals. "I hung a worm," he says, "head downwards in a long cylindrical glass full of water, and with its posterior end attached to a thread over the margin of the glass, and watched it. First it stretched out its head-bladders (suckers, see Fig. 223) like the horns of a snail, as I previously observed in a segmented cystic worm from the liver of the mouse (*Cysticercus fasciolaris*, Fig. 202). Then the border of this upper part which was hanging down became for a short time crumpled, so that it looked like a Savoy cabbage; but this movement did not last long. Thirdly, it made a manœuvre which astonished me. Feeling apparently that the water was not its native element, it tried to get out. *With the lower rim of the last joint of the outside portion it firmly fixed itself to the glass.* Then with incredible rapidity it contracted into a few lines the contiguous stretch of joints which were partly under water. The breadth was thereby very considerably increased to almost an inch, and this whole stretch of joints was lifted out of the water. The formerly fixed joint was then relaxed, and the contracted portion elongated again, so that it now hung over the glass. In the same way the middle portion, and finally the cephalic end, were lifted up out of the water. In three contractions it lay onthe ground near the glass. From this movement we can understand how a worm, especially a human one, can work its way back into the intestine, even when it has been so far expelled that a long piece of it hangs out from the rectum or anus."

considerable distance (3 to 4 mm.). From this main stem there spring on either side about twenty to thirty branches, which succeed each other at short distances, and with few exceptions extend over the whole of the middle portion to the inner boundary of the cortical layer, close to which they all end blindly. If we except the terminal branches at each end, they all spring almost at right angles from the main stem, only bending occasionally forwards or backwards, and exhibiting many minor twists corresponding to the numerous secondary divisions which they give off in their course. The number of definite branches is about eighty and more, but it must also be noted that the side at which the peripheral pore is situated has always a somewhat smaller number, since two lateral branches have usually been replaced by the vas deferens and vagina about the beginning of the posterior two-thirds of the proglottis. The proximal and distal primary branches have their processes bent round from the transverse direction towards the ends of the proglottis, to which those in the longitudinal axis are indeed almost at right angles. This is of course most striking at the posterior end, where both the branches themselves and their processes are of considerable length, and are grouped on either side in an almost fan-shaped manner. The triangular space remaining in the middle between the two halves is only incompletely occupied by longitudinal ramifications.[1]

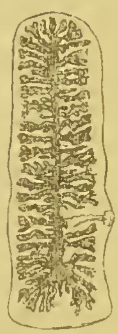


FIG. 242.—Uterus of a free proglottis. (× 2.)

It is hardly necessary to note that the eggs, lying somewhat freely within the uterus, are very unequally distributed according to the direction of the muscular pressure. Sometimes one branch, sometimes another, is specially full and distended, and the blind ends are not unfrequently swollen like clubs. But the characteristic appearance of the uterine ramifications is never hidden, nor are the distinctions obliterated which obtain between this species and *T. solium*. The most hasty comparison of the structure of the uterus in the two is, as a rule, quite enough for correct diagnosis.

I say, as a rule, for sometimes it must be allowed that there is a certain variability in the structure of the uterus. On the one hand, there are cases of *T. solium* in which the lateral branches of the uterus are more or less abnormal in number, and on the other hand, I

[1] The first satisfactory observations on the nature of the uterus in *Tænia saginata* are those of Platner, who has given us a thorough if not exhaustive account of the structure of the generative organs; "Anat. Untersuchungen über den menschlichen Kettenwurm," *Müller's Archiv f. Anat. u. Physiol.*, p. 275, 1859.

have seen specimens of *T. saginata* in which the formation of the uterus, owing to reduction of its lateral branches and the obliteration of the accessory twigs, somewhat resembled that of *T. solium*. Yet I must assert that I have never been in the least doubt as to the great majority of the preparations and worms which I have examined; not even in the case of the worm which I have represented as faithfully as possible in the accompanying figure. In spite of the comparatively simple structure of the uterus, I considered it from the first as *T. saginata*, and the corroboration of my diagnosis was finally furnished by the expulsion of the head. The joints of this (unpigmented) worm were all of the above structure, indeed I have never found a tape-worm all the segments of which were not uniform in this respect.

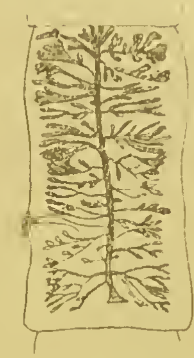


FIG. 243.—Joint of a *T. saginata* with unusually simple structure of the uterus. (× 2.)

Whether or not the simplification of the uterus in *T. saginata* may go still further, must remain uncertain. Weinland reports having found an American tape-worm which in size and head-structure belonged to this species, and yet had exactly the uterus of *T. solium*.[1]

Of course it is not only the proglottides which are capable of great mobility and contractility. The whole tape-worm possesses these properties in a corresponding degree, as is to be inferred from the uniform arrangement and development of the musculature throughout the chain.

Such being the case, the measurements of tape-worms yield very varied results, according to the state of contraction. We have given the length of *Tænia saginata* in our diagnosis as from 4 to 8 metres,[2] and have explained the reported variations as due to the varied extension of the worm, but we must also note that the varying number of ripe proglottides has also much influence in determining the length. On the other hand, we should have only a very incomplete idea of the effects of muscular action if we were to limit them by stating that the extreme dimensions are in the ratio 1 : 2. Göze saw a portion of a

[1] "Essay on the Tape-worms of Man," p. 40, Fig. 8, Boston, 1858; *Med. Corresp.-Bl. d. würtemb. ärztl. Vereins*, p. 31, 1859.

[2] According to Bremser and Diesing, the famous Viennese collection of Helminths contains chains 20 to 24 feet long, very much longer, therefore, than the preserved specimens I have measured, which were at most only slightly above 14 feet. Bremser reports having seen still larger worms. The older results, according to which *Tænia solium* (*i.e.*, generally *Tænia saginata*) grew to 40, 50, and even 800 yards, are generally regarded as erroneous. They have apparently added up every portion of the worm at any time evacuated, and thus attained a result so colossal that it could not be contained at one time in the human intestine.

large tape-worm from the cat (which is not more muscular than the *T. saginata*), six inches long, contract "with incredible rapidity" to a length of a few lines, and the whole worm, after having been only three inches long, when put into lukewarm water extended itself again to a yard and a quarter.[1]

The contraction is not uniform over the whole length. One sometimes sees, indeed, that the whole worm shortens powerfully and suddenly, if it be, for instance, rapidly transferred from the warm intestine to cold water or spirits. Similarly, one sometimes sees a wave of contraction pass continuously backwards or forwards over a long series of joints. Not less frequently do we find that the play of motion is confined to a short portion, or to a few joints, which thus manifest before their separation that morphological and anatomical independence which is also (see p. 293) expressed in the arrangement of the muscles of the body. Not unfrequently one finds neighbouring portions and joints in quite different states; some broad and much contracted, others long and drawn out into thin bands, and may even observe that not only the anterior and posterior ends, but the two sides of the same segment, are in form and motion somewhat independent of one another.

We need not emphasise the close connection between the number of the ripe proglottides and the length of *Tænia saginata*. The number varies greatly in different cases. Even the number of proglottides expelled daily from the affected patients may vary from seven or eight up to twelve, although the growth is on the whole very uniform, a head producing in about three months a chain of about 1300 joints, and therefore about fourteen daily. It is thus evident that the number of ripe proglottides would be continually on the increase, were it not that there occurs from time to time a specially copious expulsion.[2] On the other hand, we must also take into account that the formation of new joints in the adult tape-worm will perhaps occur less rapidly than was the case during the development of the chain, for in the adult the relation of the nutritive absorptive surface to the growing mass is ever becoming more unfavourable. It is possible, further, that varying nutritive conditions may in some cases determine an unequal growth.

The general growth and gradual increase in size of the joints, and their influence upon the appearance of the worm, may be most conveniently discussed by taking a concrete example. I will, in the first place, refer to a specimen in the collection at Leipsic, which in a comparatively contracted state measures 485 cm., and is com-

[1] *Loc. cit.*, pp. 345-346.
[2] This supposition is confirmed by the results of Schimper's experience in Abyssinia.

posed of 1318 joints. Close behind the head, which has a size of 1·7, the neck is 0·8 mm. broad, and at a distance of 5 cm. it has grown to 1·5 mm. The first 6 to 8 mm. are destitute of any clear segmentation, but after that the segments follow each other so closely that 270 can be distinguished within the 5 cm. just referred to. In spite of this very considerable number, the last joints have a length of 0·5 mm., which by the end of the second length of 5 cm. (380th joint) has risen to 0·8 mm., with an associated breadth of 3 mm. The next 25 cm. contain fewer joints than did the first 10—viz., 247, of which the last are 1·5 mm. long by 5 mm. broad. Henceforward the size rapidly increases, while the number of joints sinks in proportion. Thus, taking successive lengths of 50 cm. each, we have the following results :—

36— 85	cm. contained	180 joints,	of which	the last was	4 mm.	long by	10 mm.	broad.
86—135	,,	135	,,	,,	4·5	,,	12·5	,,
136—185	,,	107	,,	,,	5	,,	13·5	,,
186—235	,,	91	,,	,,	6	,,	14	,,
236—285	,,	83	,,	,,	7	,,	13	,,
286—335	,,	64	,,	,,	9	,,	12	,,
336—385	,,	53	,,	,,	14	,,	7·3	,,
386—435	,,	48	,,	,,	15	,,	7	,,
436—485	,,	30	,,	,,	19	,,	5	,,

The last 249 cm. contain not more than 278 joints—a marked contrast to the anterior 235 cm. in which there were 1040. The above measurements also show that the greatest breadth occurs about the middle of the body. From that point it decreases both anteriorly and posteriorly, and posteriorly although the length always continues to increase, which is to be regarded rather as the result of an extension than of growth. It is only in the last 100 joints that the length exceeds the breadth.

When the state of contraction alters, then the relation of length to breadth must also alter. We can best perceive this by direct measurement, such as is again afforded us by a much contracted specimen only 206 cm. long in the Zoological collection at Leipsic.

The contracted state of this worm is most plainly seen at the neck, which passes anteriorly without any marked decrease in size into the head (which measures about 2 mm.), and at a distance of 6 cm. behind possesses a breadth of 4 mm. The segmentation can be followed almost to the head, although the number of the segments is at first difficult to determine. I do not think, however, that I am far from the true facts of the case when I credit the foremost centimetre with about 200 segments. The number is greater than that of the succeeding 5 cm., which only exhibit 186. The length of the joints has, however, increased proportionally, rising from 0·1 mm. at

the beginning of this series of joints to 0·5 mm. at the end. Twenty-five cm. further back, and therefore at a distance of 31 cm. behind the head, the breadth of the body has increased to about 10 mm. There were 376 joints in this length, but the greater part of these were in the anterior 12 cm., for the length of the joints increases posteriorly very nearly up to 2·6 mm. The remaining 150 cm. were composed of 321 segments, of which the three successive lengths of 50 cm. contained 170, 91, and 63 respectively. The length and breadth of the last segment of each division were expressed by the following ratios:—4·3 : 11·5, 7 : 11, 12 : 6·5.

The total number of segments in this worm was about 1083, but it is not perfect, having lost its posterior end, perhaps in connection with the strong contraction which it has undergone. A comparison with the worm first measured would lead us to conjecture that this end measured about 200 cm., and was composed of perhaps 200 proglottides, so that we may fairly attribute to this animal a length of about 400 cm., and about 1300 joints.

Earlier computations all fall short of this result. In the first edition of this work, at a time when I had seen no perfect specimen (with the head), I estimated the number at about 1000. Dr. A. Schmidt in Frankfort counted on a worm of "not very great size" 1058 joints, including 100 ripe proglottides, and Sommer, who has most intimately examined the *Tænia saginata*, fixes the number at 1221. The differences seem more considerable than they are in reality, for they result simply from the circumstances that the anterior segments, which can only be made out with difficulty even with the microscope, have been left out of account, and that the computation has in fact begun at a varying distance behind the head.[1] But a single centimetre sometimes makes a difference of more than a hundred joints. And since neither Schmidt nor Sommer have given any detailed report as to the nature of their "first" joint, I think we may assume that the most anterior portion has been left out of account. An absolutely correct computation is thus impossible, for the segmentation begins so gradually that the determination of the first joint is an exceedingly doubtful matter.

The boundaries of the individual joints are marked at first by simple furrows. These, though at first but shallow (Fig. 244), afterwards become somewhat deep, and are not exactly perpendicular to the long axis of the worm, but rather inclined forwards at an acute angle, so that the posterior border of one segment overlaps the beginning of its successor like a cuff. The arrangement may indeed

[1] Küchenmeister in his first work (p. 112) describes the foremost joint of his *Tænia mediocanellata* as 1 mm. long by 3 broad.

be compared to a joint, the anterior portion of each segment fitting into the preceding one like the head of a bone into its socket. We have already noted the histological peculiarities of this connection (p. 293). Posteriorly the relative size of this connecting portion decreases, and that the more conspicuously as the joints increase in size, until finally in the free proglottides it becomes hardly distinguishable.

We need hardly specially mention that the boundaries of the segments are not to be confused with the transverse furrows which traverse the surface, especially in the much contracted condition. It is indeed only in regard to the short somewhat less developed anterior joints that this confusion is possible, for posteriorly the projecting borders of the joints (which are of considerable length, of 0·5 mm. or more), render any such mistake impossible. At first the segments exhibit only a single transverse furrow, which runs across about the middle, and can be followed into the developing porus genitalis; afterwards, when the joints become longer, the number of these furrows increases, until they finally disappear in consequence of the longitudinal elongation.

FIG. 244.

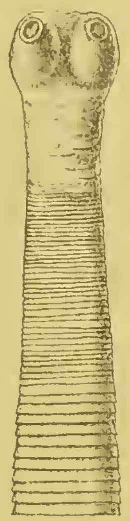


FIG. 245.

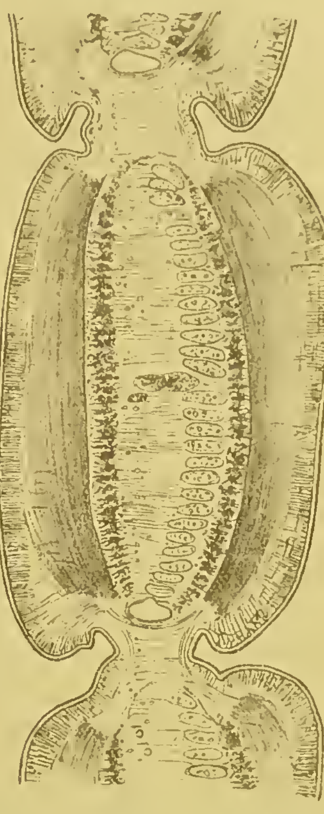


FIG. 244.—Head of *T. saginata* in a state of contraction. (× 8.)
FIG. 245.—Longitudinal section through *T. saginata* (a young chain). (× 25.)

The Development of Sexual Organs, as well as that of other parts of the body, is associated with the increase in size of the segments in a manner to which we have already alluded. It is more than a mere temporal relation that obtains between the two processes. The formation and development of the sexual organs have a most unmistakeable influence on the form of the joints and of the whole chain. This is most evident in connection with the specially long or extended joints, which owe their particular shape in great part to processes occurring within the uterus, and essentially amounting to this, that the eggs, with their maturity, attain at the same time their maximum size, and then collect principally in the median longitudinal stem.

The first rudiments of the sexual organs appear somewhat early, in about the 200th joint. The processes of formation and growth, as observed by Sommer, are very like those which I stated in the first edition of this work, in regard to *T. solium*. The full development of the reproductive organs is signalised and completed by impregnation and passage of the eggs into the uterus. These two events are separated from one another by a distance of about a hundred joints. The development progresses over almost 450 joints, for the first egg in the uterus is observed about the 640th.[1] Shortly before copulation, which takes place at the 516th joint, the porus genitalis and its papilla are formed, whilst the peripheral depression is visible about 100 segments earlier.

The proper sexual maturity occurs when the chain has acquired about half its total number of joints, at a point which is indeed far from representing the middle of the adult worm, but in fact, in the above-mentioned specimens, lies only about 30 to 38 cm. from the head. The joints concerned are all characterised by a very appreciable and disproportionate increase in breadth.

This state of matters alters as soon as the eggs pass into the uterus. The median canal, which at this time constitutes the whole uterus, stretches out increasingly as it becomes packed with eggs. In consequence of the pressure, the form of the joint becomes approximately rectangular, and that the more markedly, as the number of eggs continues for a good while to multiply, and, with the incipient embryonic development, their size becomes greatly increased. The uterus, however, does not remain a simple tube; at the 700th joint, at the point where the formerly abundant testes begin to degenerate, a number of protuberances appear at the sides of the tube. These elongate into the space which now becomes free, and as the testes disappear, the uterine processes finally occupy the whole space. The eggs continue to be pushed forward on to the 930th joint, up to which point the female germ-producing organs still retain their full development. Afterwards they too become wasted, and then only do the branches of the uterus begin to assume their final form. At this time, too, one even finds some eggs with hook-bearing embryos; but the number of these is small at first, till 150 segments further back it begins to increase until the 1100th. Here by far the greater number have gone through their primary metamorphosis, and are inclosed in the embryonic shell.

The full development of both eggs and uterus occurs, of course,

[1] My computations differ somewhat, as I have explained, from those of Sommer, who finds the first rudiment of the sexual organs in the 140th joint, the impregnation in the 482d, and the first occurrence of eggs in the uterus in the 581st.

only in the last portion of the chain, where the demands for space made by the young brood reach their maximum, and the proglottides gradually prepare for their liberation by the continued contraction of their transverse musculature.

The Head.—Passing to the consideration of the parts of the body in detail, we may first note that the head is comparatively large, and distinctly recognisable by the naked eye. In one of my specimens the head was about 2 mm. broad, by about 1·5 thick. Other specimens, it is true, fall far short of this, and since this smaller size is most marked in the bladder-worms, one of which had a head measuring hardly 1 mm., we may infer that the age of the worm is an important factor in determining the size of the head. The head of *Tænia saginata* only reaches its full developement subsequently during the tape-worm stage.

But it is not the size merely which varies in the different forms. The form and nature of the neck also vary according to the state of contraction. Even Bremser notes that the latter is in constant motion, and retains the form it possessed at death. When the worm is suddenly killed when in an active state of vitality, the neck is found shortened and broad, almost as broad in fact as the head, which at first sight looks exactly like the truncated end of the neck (Fig. 246 *A*). On the other hand, the specimens killed slowly in some more indifferent fluid have a long slender neck, which passes backwards, gradually broadening into the jointed body, while in front it is sharply separated from the head. The latter appears in such cases as an independent appendage of an almost pear-like shape, somewhat flat in front, with rounded border, and a narrow conical basal portion attached to the neck as to a stalk. The largest part of the head is occupied by the cylindrical suckers which measure 0·8 mm. in diameter. After death these are generally retracted; while in life they are frequently protruded "like a snail's horns." Their openings are usually greatly narrowed, so that they come to have little more than the third of their equatorial diameter. In the specimens I examined

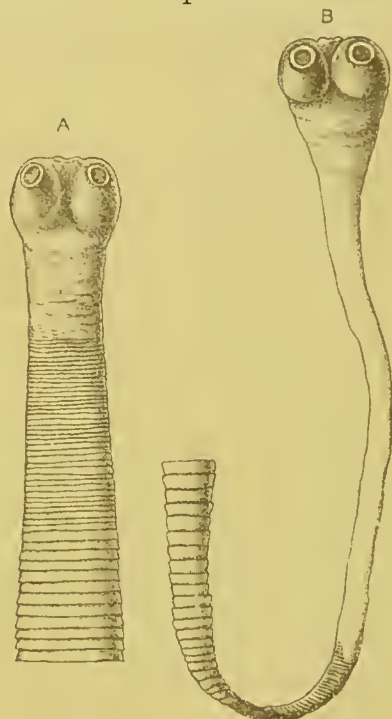


FIG. 246.—Cephalic end of *Tænia saginata* in retracted (*A*), and extended state (*B*). (× 8.)

they were always directed forwards, so that the muscular mass of the sucker thus came to lie behind the openings, embedded in the parenchyma of the head, whose form was essentially determined by this circumstance.

Histologically the suckers only differ from the ordinary type in the special strength of their musculature. The walls have an unusual thickness, and are so firmly united that they can be separated from their surroundings by even gentle pressure.

But the size and strong development of the suckers are not the only distinctive features in the structure of the head. The absence of the circlet of hooks is not less noteworthy, and determines the remarkable flattening of the apex, which is in such contrast to allied forms; the apical surface of the worm being in no case, however, perfectly level.

Even Batsch mentions in his *Tænia dentata* a "media papilla" of small size lying between the suckers. Similarly, Bremser [1] saw at this point "an arched protuberance on which one always notices a circle with a small, hardly perceptible, opening in its centre." He regards this circle as rostellum, as may be inferred from the further observation, that it "often, but not always" (that is in *Tænia solium*, but not in *T. saginata*), bears a double circle of hooks.

I have since shown the truth of this identification.[2] *T. saginata* does indeed possess a rostellum, as has been amply confirmed both by Nitsche and Moniez.[3] The rostellum is, however, but a small one (0·25 mm.), though essentially agreeing with that of related forms. It consists of a well-defined lenticular body, mainly composed of fibres, which are stretched straight between the two opposite surfaces. They have thus a longitudinal course, and are crossed posteriorly by a system of radial fibres. The muscles which usually run along the under part of the rostellum are only slightly differentiated, and are hardly recognisable as distinct structures, though in arrangement and course they certainly resemble those of allied forms.

So far, then, the rostellum of *Tænia saginata*, in spite of its comparatively weak development, possesses essentially the structure seen in the hook-bearing cystic tape-worms. But, while in the latter the rostellum is covered by a prominent layer of parenchyma

[1] *Loc. cit.*, p. 100. Bremser refers there to his figure (Tab. iii., Fig. 3). This is to be referred to *T. saginata* and not to *T. solium*, as Küchenmeister would have it ("Parasiten," 2d ed., p. 153, note). It was taken from a living hookless specimen by Bremser in Vienna.

[2] First German edition of this work, Bd. i., p. 409.

[3] Küchenmeister says that this structure has been "first accurately described by Landois and Sommer," but he forgets to say where. In the well-known paper on *T. mediocanellata* it is not mentioned at all.

in which the anterior processes of the hooks are embedded, this coating is represented in *T. saginata* only by an annular diaphragm, which lies as a lip on the outer wall of the above-mentioned lenticular mass. This is more or less markedly arched according to the curvature of the latter, and has in its centre an opening which is expanded below, and appears sometimes rather deep, since the lenticular body has not unfrequently a depression in its anterior surface. This is the opening long since observed by Bremser, and occasionally by other observers, and the appearance of which has given rise to the formerly prevalent idea that the tape-worms possessed a mouth opening between the suckers.

FIG. 247.—Head of *Tænia saginata* in longitudinal section. (× 25.)

I have already noted (p. 351) that the peculiar formation[1] of this structure, as above described, may also be observed at a certain stage in the development of the hook-bearing cystic worms, where it attains its final organization after the hooks and their root-processes have been formed. The state of affairs in *T. saginata* is therefore far from interrupting the unity of type found in other forms. It either represents in a permanent form the early phase, which has remained undeveloped, or it is the result of retrogression.

The resemblance is further increased by the fact that the border of the diaphragm in *T. saginata* is also at first provided with a close circle of little points, that is, with structures such as we saw to be the first traces of the hooks. But the points do not develop, they retain their primary form, and very soon disappear. Nitsche notes, however, that occasionally some of these rudimentary structures persist round about the central pore of the head.[2]

In the first edition of this work I regarded this pore, which I called the "frontal sucker," along with the muscular apparatus lying below it (the rostellum or "bulbus"), as the morphological equivalent of that sucker which is found between the lateral suckers, not only in Rudolphi's *Scolex* (p. 371) and the associated Phyllobothria, but also in some Tæniadæ. It must not be supposed from this that the

[1] Unlike Küchenmeister, who finds this structure "sometimes but not always" in *Tænia saginata* ("Parasiten," 2d ed., p. 180), I have always found it when I looked for it in the right way, and must therefore regard this rudimentary proboscis as a constant character of this worm.

[2] Küchenmeister's statement ("Parasiten," 2d ed., p. 180) that Heller has seen twelve, sixteen, or even thirty-two short thick hooks on the head of *Cysticercus bovis* is incorrect. Heller's observations (see p. 319) referred to many-hooked embryos.

homologous rostellum of the hooked tape-worms agrees in every particular with a sucker; yet although this is as clearly stated in my former observations, as now, Küchenmeister seems to have misunderstood my comparison of the two structures, for he characterises it in his recent work on parasites sometimes as "unfortunate" and sometimes as "incorrect." I can hardly suppose that these epithets will utterly condemn the alleged homology, for this has been, as Moniez emphasises, established beyond doubt by the developmental history.

The black coloration, which was long ago observed by Andry, and which occurs much more abundantly in *Tænia saginata* than in *T. solium*, is caused by a granular pigment which is embedded in the connective tissue, and is sometimes found even within the cells. Here and there, according to Virchow, it has a crystalline character. Where it occurs only sparsely it is usually found restricted to the neighbourhood of the suckers, but is sometimes spread over the whole head. Davaine describes as a special variety a perfectly black tape-worm ("Ténia nègre") from the Southern States of North America.

As to the nature of this pigment, nothing certain is known; but it is probable that it originates from the colouring matter in the blood of the host, and therefore has the same origin as the pigment of the latter, having a close resemblance to melanin. Its origin can hardly be as simple as Küchenmeister would have it, when he supposes that those blood-corpuscles which are taken in by the pores of the suckers, and are not used, become changed directly into pigment.[1] This can hardly be, for the ingestion of blood-corpuscles through the suckers of the *Tæniæ* is more than doubtful on anatomical grounds (p. 304); and further, it must be noted, that this embedded pigment is found occasionally even in the bladder-worms, that is, in organisms which are hardly in a position to devour blood-corpuscles as such. In *Tænia saginata,* indeed, I have not yet noticed these black-headed bladder-worms, but they are to be found in *T. solium,* which is, however, on the whole much less copiously provided with the pigment. For this reason I think I am justified in assuming that the presence and distribution of the pigment stand in no definite relation to the age of the worm.

We have already noted that the pigment is not found exclusively on the head, but occurs occasionally on the vagina, vas deferens, and testes. This is the case, however, only in the older proglottides, where the organs in question are no longer functional.

In such ripe joints one sometimes finds in the cortical sheath accumulations of granular molecules, and also yellow fat-drops, some-

[1] *Loc. cit.*, p. 151, note.

times in such abundance that the sides exhibit green streaks. This was specially striking in the case of two *Tæniæ*, which one of my Russian pupils, now Profęssor P., acquired five years ago in St. Petersburg, and in which all the proglottides (twelve of which were voided daily) were provided with a green border.

As to the rest of the organization, there is little, except in regard to the sexual organs, which calls for detailed discussion. We have already mentioned the specially powerful musculature and the very energetic movements. As to the course and arrangement of the fibres, we need only remind the reader that *T. saginata* was the example we chose as a general type in our detailed description.

FIG. 248.—Head of *Cysticercus Tæniæ saginatæ*, with frontal sucker and vascular ring. (× 30.)

I cannot exactly confirm the results at which Küchenmeister[1] has arrived in regard to the vascular apparatus of his *Tænia mediocanellata*, according to which it is much simpler in the head than is the case in *T. solium*. It is indeed true that the ring round the rostellum is, as one would expect, but narrow, yet its structure and arrangement are, for all that, quite normal. Similarly, the four longitudinal canals which form the ring are different only in this respect, that the number and development of the branches are in fact greater than

[1] "Cestoden," &c., p. 110.

usual. The calcareous bodies of *T. saginata* are also, on an average, larger (up to 0·018 mm.), and more abundant than in *T. solium.*

The Structure of the Sexual Organs is best observed in joints of medium size (8 to 10 mm. broad by 4 to 6 mm. long), which are in a moderately contracted state approximately rectangular, and belong to the second half of the seventh hundred. They are found, according to the state of contraction, at a distance of about 40 cm. behind the head. They show the generative organs of both sexes in full development. The copulation has just taken place, and the eggs are beginning to pass into the uterus.

For the purpose of closer examination the fresh joints should be left for a day in ammoniacal solution of carmine of medium concentration. After being clarified in glycerine or balsam, one can see on slight pressure all the parts with great distinctness. Apart from the ducts, this is specially true of the female organs, which, with the exception of the median uterus, all lie in the posterior half of the proglottis, and are quite perceptible by transmitted light even to the naked eye. To examine the more intimate structure it is necessary to have recourse to sections, especially to horizontal ones.

The Male Organs.—In detail one may note the following characters:—

The Testes are first ripe, and consist, as in most Cestodes, and especially in the larger species, of numerous roundish vesicles, which measure on an average about 0·15 mm. (from 0·12 to 0·18), and which fill up all the vacant space in the joint within the vessels. In the anterior half of the joint they are of course much more numerous than behind, where the female generative organs occupy most of the space. Here they are found chiefly at the sides, as is also the case in the anterior half. The vesicles are therefore larger and more advanced along the two sides than the middle of the joint.

The contents consist partly of long thin adult spermatozoa, which are curled up together in bundles, and usually lie near the wall of the vesicle, with their otherwise hardly defined heads resting on a granular mass. There are also small round balls of varying size up to 0·043 mm., which contain numerous small cells, and represent the early developmental stages of the seminal elements. In the larger balls one can distinctly observe a large clear sphere (0·03 mm.) on which the cells are seated—a structure which often occurs in the lower animals as the bearer of the sperm-cells proper. The cells which lie on this to a greater or less extent (nuclei, according to Sommer and Landois), may be observed growing into spermatozoa, while the central sphere itself finally becomes the above-mentioned granular mass.

In the small less defined testicular vesicles one finds, moreover, simple nucleated cells, which by growth and endogenous multiplication produce the above-mentioned elements.

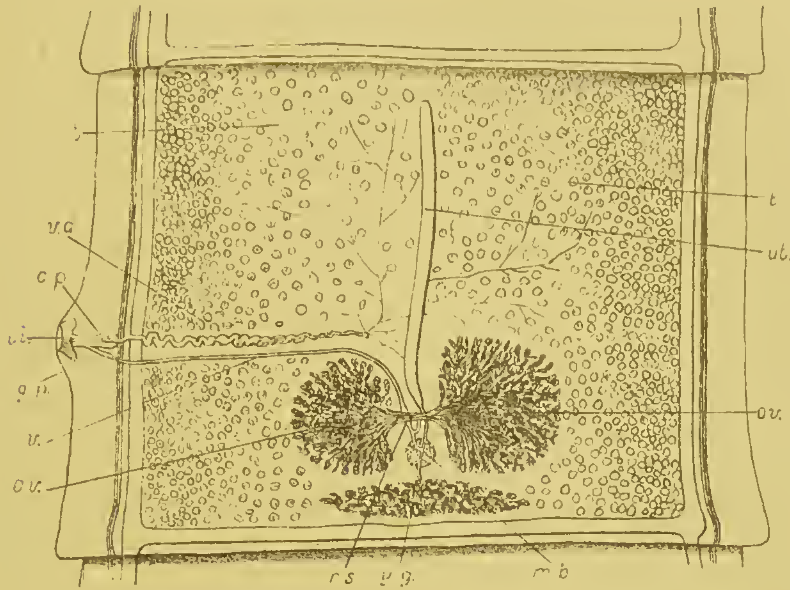


FIG. 249.—Generative organs of *Tænia saginata* (× 10.) Male organs.—*t.*, testes; *v.d.*, vas deferens; *c.p.*, cirrhus-pouch. Female organs.—*ov.*, ovary; *y.g.*, yolk-gland; *m.b.*, shell-gland (Mehlis' body); *r.s.*, receptaculum seminis; *ut.*, uterus; *v.*, vagina; *g.p.*, genital papilla; *cl.*, cloaca.

The testes, when full of ripe spermatozoa, have their original spherical form modified, inasmuch as they are each drawn out at one point into a pointed process, by means of which they are fixed like berries to the ramifications of the vas deferens. The latter is quite conspicuous as in other Cestodes, and its course across the joint from the porus genitalis to the uterus can be followed even with the naked eye, but the processes are, on the contrary, seldom seen with great definiteness. To the older anatomists both they and the testes were alike unknown, and, till F. S. Schultze's discovery, the latter were very generally identified with the vas deferens.

In favourable specimens we can observe that these processes proceed wholly from the posterior end of the vas deferens. This is seen (Fig. 249) to be continued into a number of thin canals which run in an almost radiate manner from the point of origin, and break up into finer twigs. The majority of these canals belong, of course, to the anterior half of the joint, but some also run backwards. Here and there they become almost varicose by the accumulation of spermatic elements within them. This can be occasionally seen even in the ripe proglottides where the testes have long since degenerated, and

even in some which have spontaneously left the intestine and voided their eggs. This varicose enlargement is to be seen most frequently near the point where they open into the vas deferens or just at the junction, and has been described by Platner, to whom we are indebted for the most thorough representation of these structures, as a special hollow of irregular jagged form—the "spermatic sinus."

The Vas Deferens itself is a comparatively wide canal with a diameter of about 0·025 mm. It runs from the external aperture—the porus genitalis—across the joint almost as far as the uterus, yet not in a straight course, but, as in related forms, with numerous more or less close coils, which sometimes look as though they were enclosed in a common sheath. I have never been able to observe any special enlargement or seminal vesicle either in the vas deferens or inside the cirrhus-pouch into which the former opens. In the posterior somewhat distended portion of the bottle-shaped cirrhus-pouch (about 0·4 – 0·5 mm. long) are found a few irregular windings of the vas deferens, which does not exhibit here its usual thick firm walls, but is clad internally with a thick layer of fine chitinous points directed backwards. This structure is obviously adapted for protrusion during copulation, forming the so-called "cirrhus."

The Cirrhus in *Tænia saginata* is very short, so that one only sees it slightly protruded from the porus genitalis. It must, of course, be remembered that the porus genitalis of this worm leads first into a deep (0·22 mm.) wide pouch or funnel-like cavity, which I have called the "generative cloaca," because, besides the vas deferens, the vagina also opens into its narrow posterior end.

The Cloaca originates by the external body-wall becoming swollen into an annular lip round the common generative opening. In consequence of this the pore comes to lie at the end of a sort of boss-like protuberance, as in most of the other *Cystotæniæ*, but here it is unusually large, up to 1 mm. Transverse sections through the generative cloaca leave not the slightest doubt as to the nature of the swelling. One sees not only (Fig. 144) how the cuticle is continued almost unaltered into the interior, but can also follow the musculature of the cortical layer out into the surrounding walls.

My former statements, according to which the pore was surrounded by a special sphincter, which shut off the internal cavity during copulation, have been corrected by Sommer and Landois. In reality one sees in the wall of the generative cloaca no muscular elements other than the processes of the transverse fibres bounding the inner layer, which, instead of intertwining, run out to the outer surface of the cirrhus-pouch, and sagittal fibres, which penetrate the projecting lips in a dorso-ventral direction. But in spite of the absence of a proper

musculature, the generative cloaca is able to undergo manifold changes in form and width, and thus to narrow or widen its opening. These changes occur mainly in consequence of the pressure and traction of the adjacent body muscles.

We can the more rapidly dismiss the muscular structure of the cirrhus-pouch, since it was especially *Tænia saginata* which we had in view in our general account of this organ (p. 310).

The peripheral layer which the pouch possesses leads one to suppose that it is in the cortical layer that the cirrhus-pouch has arisen. This cannot indeed be demonstrated with certainty, since the above-mentioned course of the transverse fibres obliterates the boundaries between the two layers of the body. The nerve cord and the longitudinal vessel, which are both distinctive of these layers, lie internally to the cirrhus-pouch, but are divergent, inasmuch as they are not close beside each other, but are approximated to different surfaces of the body—the longitudinal vessel towards that which we have formerly called the "female," and the nerve cord towards the opposite or "male" surface. The cirrhus-pouch is also more or less distinctly approximated to the latter, whether the pore be on the right or left side of the body.

Although the situation of this pore varies extremely, lying always on one side for perhaps six or eight joints, and then alternating almost regularly throughout another series, yet there is on the whole but little difference in this respect between the two sides. In a length of 100 joints I counted 56 pores on the left, and 44 on the right.

Whether the pore lie right or left, one always finds it at some distance behind the middle, and that the more markedly the longer the joint. In isolated proglottides 12 mm. long, it lies fully 7 mm., and sometimes even more, behind the anterior border.

The Female Organs.—The narrow funnel-like end of the generative cloaca contains not only the male opening with the copulatory organ, but also, as we have seen, the female opening. This is so closely approximated to the former, that the cirrhus can easily bend round into it when the pore is closed. I have seen this take place in *Tænia echinococcus* and other species from the dog, and therefore I presume it happens also in *T. saginata.*[1] The semen, thus introduced into the female organs, first passes through the slightly enlarged terminal portion into the vagina. This is a long and thin (0·025 mm.) canal, which pursues for a while a straight course below the coiled vas

[1] I have already (p. 310, note) mentioned that Sommer denies the entrance of the cirrhus into the vagina, and asserts that the semen simply overflows into the female opening without any true copulation. He thinks that I have been misled in my observations by a stream of spermatozoa.

deferens, but bending downwards (Fig. 250) in a somewhat sharp curve, ends in the middle line, half-way between the end of the uterus and the posterior border of the joint.

The Vagina, like the cirrhus and vas deferens, is lined by a continuation of the cuticle, but its walls possess considerable power of resistance, and are thicker than those of the vas deferens, so that the lumen measures scarcely more than 0·018 mm. It is plain, therefore, that the vagina could not possibly receive and transmit the eggs, which, even after the loss of the external envelope, are double the above-mentioned diameter. We have, however, already noted that the eggs of the Tæniadæ only gain the exterior when the body-wall bursts—usually at the anterior border.

The Receptaculum Seminis, which is recognisable by its contents, may be seen, just where the vagina reaches the posterior end of the uterus, as a small swelling (0·1 mm. long by 0·07 mm. broad). It may be considered as occurring in the course of the vagina, although its connection with the latter, both anteriorly and posteriorly, exhibits several peculiarities. While the anterior portion of the vagina is narrow and lined with chitin, perhaps to serve as a channel for the transmission of the spermatozoa, the continuation posteriorly is wide and thin-walled—so different from the vagina proper, that we are almost justified in regarding it as a special organ. Since it conducts the spermatozoa to the ova, we have previously (p. 314) suggested the designation "fertilising-canal" ("Befruchtungs-canal") as not inappropriate for it.

The Shell-Gland.—The canal just mentioned leads in its wide course first to a spherical body about 0·2 mm. in diameter, which lies some distance behind the uterus, in fact just where the vagina ends.

Even Mehlis[1] and Platner noticed this peculiar body, but had only very imperfect knowledge of its nature and connections. Platner took it for the ovary. As a matter of fact, the body in question consists of closely compressed nucleated cells 0·02 mm. in size; these are, however, by no means eggs, but glandular cells, provided with small thin ducts opening into the narrow internal cavity of the organ, which measures 0·03 mm. The regular disposition of the cells and ducts often gives the wall a radiate appearance. Since it is inside this structure that the ovarian eggs acquire their outer envelopes of yolk and shell, the shell-substance is probably the secretion of these glandular cells. Since finding a body almost identical in structure in the Distomidæ,[2] I have called it the "shell-gland," a name often used since by other observers. Sommer calls it "Mehlis' body."

[1] *Oken's Isis*, p. 70, 1831.

[2] First German edition of this work, p. 483.

It communicates further not only with the fertilising canal, but also with the germarium and with the uterus, so that it is anatomically a sort of centre of the female reproductive system.

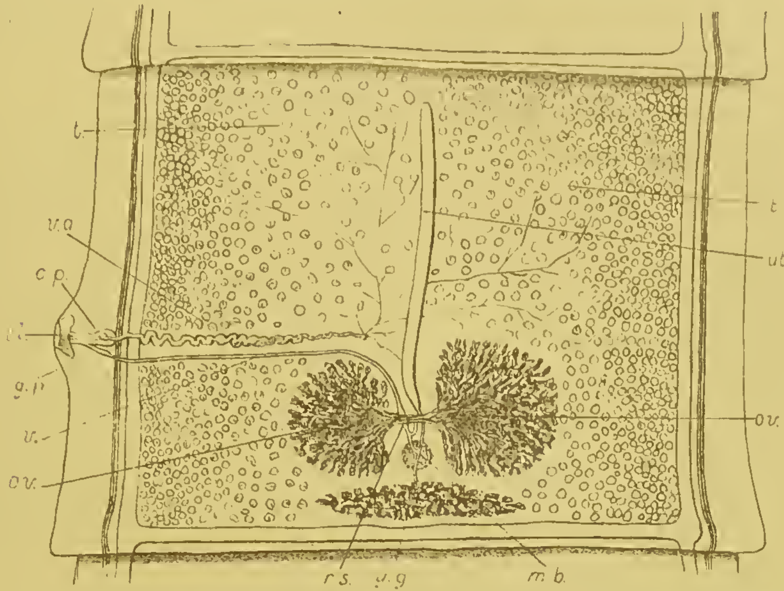


FIG. 250.—Sexual organs of *Tænia saginata* (× 10). Male organs.—*t.*, testes; *v.d.*, vas deferens; *c.p.*, cirrhus-pouch. Female organs.—*ov.*, ovary; *y.g.*, yolk-gland; *m.b.*, shell-gland (Mehlis' body); *r.s.*, receptaculum seminis; *ut.*, uterus; *v.*, vagina; *g.p.*, genital papilla; *cl.*, cloaca.

The Germ-Glands consist, as usual in the Tæniadæ, of a paired ovary and an unpaired yolk-gland. The latter, the "albumen-gland"[1] of Sommer, lies below the spherical body just described, near the posterior border of the joint, and is in the form of a triangle, which has its obtuse angle turned forwards, and extends some distance towards either side. Sometimes the inferior margin is hollowed out or even interrupted, so that it then appears almost double, as is shown in Fig. 142, representing *Tænia solium.* But such appearances are neither normal nor yet individual variations, as I was formerly inclined to suppose,[2] but are artificially produced by unequal compression.

In contrast to the yolk-gland, the ovary has the form of two large and almost round wing-like organs. They lie at either side of the receptaculum seminis, but above the shell gland, and occupying more than half the breadth of the remaining space (Fig. 250). Their height is about the third part of the length of the joint. The space between

[1] We have already (p. 320) given reasons for regarding this so-called "albumen-gland" not as an organ occurring only in the Tæniadæ, but as a form of yolk-gland widely distributed among the Platyhelminthes.

[2] I must again note (see p. 315, note) that in the first edition of this work I erroneously regarded the yolk-gland as the ovary, and *vice versa*, as has been rightly pointed out by Sommer.

them serves for the reception of the lower end of both vagina and uterus. About half-way up the wings are connected by a duct, which runs across over the receptaculum seminis. That ovary, which lies below the vagina, and is embraced by its curve, is always smaller than its fellow, which is free to extend anteriorly, and reaches not only beyond the vagina, but also beyond the vas deferens.

As to their minute structure, both ovary and yolk-gland consist of a system of blind tubules, which, as in the so-called "tubular glands," are seated on a branched efferent duct. I have never been able to observe the reticulated communication which Sommer describes between the tubules, and must say the same with regard to the coils, with branches running backwards, which Platner has described in the ovary (his "yolk-gland"). In teased preparations with low power one may indeed see appearances of this sort, but closer examination shows that the apparent network is composed of tubes lying across one another. The ends of the glandular tubules are not unfrequently widened into acini borne on thin stalks. This is specially true in regard to the ovaries, which thus acquire a somewhat less dense texture, and a more transparent appearance.

It is doubtful whether the bounding membrane of the tubules is an independent skin, as in the testicular vesicles, or merely belongs to the matrix. It is, at any rate, the only boundary of the glands. The contents both of yolk-gland and ovary consist of cells about 0·007 mm. in size, with vesicular nuclei and distinct nucleoli. On the whole, they resemble one another, but exhibit many differences on closer inspection.

The cells of the ovary (the primitive eggs) have a sharper contour, and are provided with a thin, clear, protoplasmic envelope; they have also a larger nucleus (the germinal vesicle), whilst the cells of the yolk exhibit an abundance of a finely granular enveloping mass, not unfrequently exceeding the above-mentioned normal size. They are often very irregular in form. Here and there the individual cells are hardly distinguishable. They have broken down and fused together into an amorphous secretion, in which one can distinguish only a few flakes and nucleus-like structures.

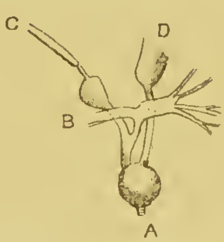


FIG. 251. — Mehlis' body in connection with the various parts of the female productive organs. *a*. Efferent canal of the yolk-gland, *b*. Efferent canal of the ovary, *c*. Vagina and receptaculum, *d*. Uterus. (× 30.)

The connection between these organs and the shell-gland can only rarely be seen with any distinctness. Its demonstration is the most difficult part of the anatomy. It is most easily seen in the neighbourhood of the yolk-gland, for its efferent

canal runs straight forward and sinks into the posterior end of the spherical body. It is much more difficult to demonstrate its connection with the ovary. In favourable preparations, however, it can be seen satisfactorily, and one can convince oneself that the efferent ducts of the tubules finally collect into two transverse branches, which after a short course meet together and then continue in a common duct, which opens into the fertilising canal. Both transverse canals seem to be very extensile; they are often seen full of eggs, and sometimes even enlarged into a distinct cavity.[1]

The Uterus, however, is also in connection with the shell-gland, by means of a thin duct (0·04 mm. wide), which springs from the gland near the insertion of the fertilising canal, and opens into the posterior end of the uterus.[2] The latter appears, in some respects, as though it were the direct continuation of the canal just mentioned. Like it, the uterus runs straight up the middle line of the joint, continuing nearly to the anterior border, where it ends blindly. Of the subsequent lateral branches there is as yet no trace. The uterus is still a simple tube, with well-defined boundary walls and considerable width (up to 0·16 mm.), so that it is sharply distinguished from the canal which leads to it. The length of the latter is not always the same in the different joints; it is on the whole but short, so that the lower end of the uterus usually projects some distance between the ovaries.

What I have just stated in regard to the structure of the sexual organs in *Tœnia saginata* is primarily true only of the adult joints, those, namely, which are about to copulate, and in which the filling of the uterus is just about to commence. But a similar state of the organs may be observed both in earlier and later stages, as was stated with respect to *Tœnia solium* in the first edition of this work. In both cases it is necessary to use the staining methods recommended above.

The Sexual Development is first apparent in joints about 2·5 mm. broad by 0·3 mm. long,[3] which lie at a distance of about 6 to 10 cm. behind the head, and belong to the first half of the third hundred. In these joints there is seen passing from the centre to the middle of

[1] For this reason they are regarded by Sommer, not as efferent canals, but as the median portion of the ovary connecting the two lateral lobes.

[2] Sommer, who confirms the above representation in all points, regards this canal, and also the lower end of the fertilising canal, as a direct prolongation of the oviduct. He gives them both the same name, and would thus have the lower end of the vagina (our fertilising canal) not only opening into the oviduct, but would make the latter coil round the shell-gland which is attached to it, and then run backwards to pass into the uterus. I need hardly note that all these differences are only verbal, and I see little reason to depart from what I have said, especially since the analogous structure in the Distomidæ seems hardly to favour Sommer's theory.

[3] I may again note that the accounts of the size and distance from the head are rendered very uncertain by the extreme contractility possessed by these worms.

one side or the other a somewhat broad streak of cellular parenchyma. At first (*A*) the stripe does not extend laterally beyond the median region of the joint, but gradually it elongates until it finally abuts

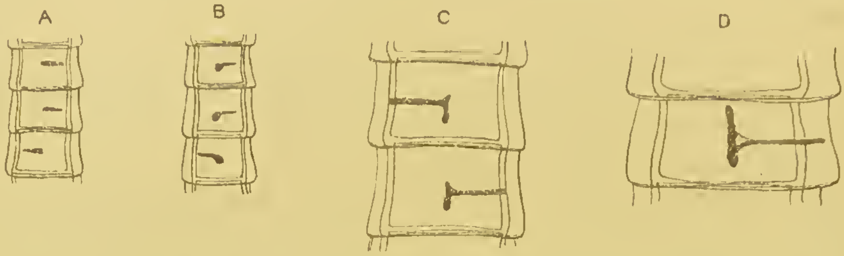


FIG. 252.—Development of the efferent generative organs in *Tænia saginata.*

against the lateral. But before this (*B*) the median end has thickened, and become a posteriorly directed club-like swelling, which gives the parenchymatous streak a certain resemblance to a pistol. The contour, which was at first somewhat vague, and which made the rudimentary structure look broad and plump, becomes more sharply defined. As the joints increase in size, the length of the parenchymatous streak increases. It becomes more slender and changes further (*C*), since the terminal club-shaped body becomes almost triangular, owing to the elevation of its anterior margin. Some centimetres further on, about 100 joints after the appearance of the first rudiment, this elevation has elongated into a streak, which can be followed up to the anterior wall, and apparently represents the first rudiment of the uterus. In the transverse streak, on the other hand, we have neither the vas deferens merely, nor the vagina, but the common rudiment of both these structures. This can be easily proved, for the borders of the streak become gradually separated, as two strands, by the clearing of the median portion and the thickening of the borders, and these, though sometimes only imperfectly separated, and still in connection with the mass of the uterus, may be distinctly recognised as vas deferens and vagina. The former is at first quite straight and destitute of a cirrhus-pouch, but that is no more difficult to explain than the absence of the generative cloaca. On the vagina there is sometimes no perceptible opening nor differentiation into the various divisions, although the posterior end is thickened like a club, and forms a swelling, which can be sharply distinguished from the adjacent parts of the uterus.

The next change in the generative organs is the disappearance of the intermediate substance, which has as yet united the vagina and vas deferens together. The two ducts thus become free, and develop independently by the differentiation of the cirrhus-pouch and the

formation of the generative openings. In joints about 4·5 mm. broad by 1 mm. long, which begin at about the fifth hundred, and are about 20 cm. distant from the head, one notices at the end of the genital ducts a discoid swelling, which encloses a shallow depression, and by its connection with the vas deferens and vagina is seen to be the genital papilla. The adjacent section of the vas deferens exhibits a long thickening, the first imperfect rudiment of the cirrhus-pouch. The coils of the vas deferens are hardly perceptible, but the posterior end already appears free, and without connection with the uterus, to which the vagina is united by its terminal club-shaped swelling, both anteriorly and posteriorly. Further, the uterus is now more sharply defined, is more slender than before, and is usually prominent opposite the generative ducts.

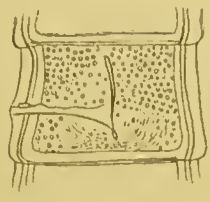


FIG. 253. — Development of the germ-producing organs. (× 5.)

The first traces of the germ-producing organs are to be found about the four hundredth joint. They are first indicated by the hitherto almost homogeneous and transparent parenchyma assuming a more granular appearance. The groups of cells of which this consists are at first but small, and of the same appearance throughout, but differently arranged in the upper and lower halves of the joints, so that one can thus early distinguish the male and female organs. In the following joints this distinction becomes more marked. The granules of the upper half become larger, and are distributed with tolerable uniformity over the whole surface of the middle region, while those in the lower half remain smaller, and become ever more distinctly arranged, so as to form distinct organs. In this way two plate-like masses arise, which enclose the lower end of the vagina and uterus between them, while very soon a third streak appears near the hinder margin of the joint. These three masses of course represent the two ovaries and the yolk-gland, while the granules of the anterior half are destined to become the testicular vesicles.

The joints in which one first sees the above diferentiation distinctly are about the 420th behind the head. In these one sees also for the first time that the conducting apparatus are distinct canals, and not solid threads. The vas deferens has a coiled course, and the posterior end of the vagina also exhibits its subsequent structure. One can recognise already in the former terminal club (Fig. 254) a differentiation into seminal vesicle and shell-gland, which for a time lie one close

FIG. 254.—Lower end of the vagina, showing its connection with the uterus. (× 30.)

behind the other. The latter is seen to be in connection with the lower end of the uterus. Similarly, one can distinguish the efferent ducts of the ovary and the yolk-glands.

From this stage there is but a step to the perfect development of the generative organs. All the parts are present; the difference is only formal, and the gradual development of the succeeding joints requires no special discussion.

The development of the generative organs is not, however, complete with the formation of the eggs and egg-glands; for the *Tæniæ* are, as is well known, distinguished from the other Cestodes in that they only produce eggs and spermatozoa during a comparatively short time, and not merely are the eggs fertilised, but the embryos proceed at once to develop in them. After the sexually mature joints there follow others, which may be termed "pregnant," and this pregnancy induces a further series of changes.

At the period of sexual maturity the uterus is a straight canal of comparatively small calibre. Its capacity is too small for the great multitude of eggs, and the more so since in the *Tæniæ* the latter grow during development to many times their original diameter. The uterus therefore begins to adapt itself to the requirements of the pregnant animal. Very soon after the transference of the first eggs it not only increases in length, but entirely changes its originally simple shape by the formation of lateral branches. The walls of the uterus give rise to small protuberances, which grow with ever-increasing rapidity, here and there bifurcate, and form secondary twigs, and finally fill up the whole breadth of the median portion as far as the longitudinal vessels. The branches are at first long and thin, and differ from their subsequent state in being longer in correspondence with the broad and short form of the joints, and also in diverging but slightly from the transverse direction.

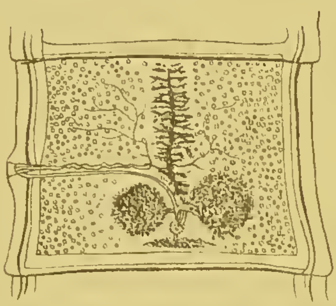


FIG. 255.—Formation of the first lateral branches of the uterus. (×5.)

For a while the male and female reproductive organs can still be seen beside the branches of the uterus. But the more the latter increase, the more the former retreat from observation. This is not so much because they are covered by the lateral branches, but is mainly due to the gradual degeneration which ensues at the close of their functional activity. This disappearance is gradual, and is not uniform, so that even in a perfectly ripe joint, remains of the reproductive organs may still persist. The female germ-producing organs persist longest, and the shell-gland so long that the development of the

posterior uterine branches is not only retarded for a while, but their form is also somewhat modified by its presence. The vacant space between the posterior fan-shaped processes represents the position occupied by the shell-gland. The unequal longitudinal development of the uterus posteriorly and anteriorly is also associated with the persistence of the shell-gland.

FIG. 256.—Eggs of *Tænia saginata; A*, Newly formed egg from the uterus; *B*, Ripe egg containing the embryo. After a drawing by Edouard van Beneden. (× 550.)

As to the development of the eggs, I have but little to add to what I have already said, which is partly based on investigations of *Tænia saginata*. I content myself with noting that the size of the embryo is about 0·02 mm. The shell which surrounds it is distinguished by considerable thickness—that is, length of the little rods which are seated on it, and which attain their full development after a very short period. Inclusive of this shell, the diameter of the egg is on an average 0·03 mm., and its form is generally oval rather than spherical. We have already noted that the eggs are also usually still surrounded by the original vitelline membrane (0·07 mm.), separated by an interval from the contents. Very frequently this outer shell is drawn out at one or at two points into a more or less long, thin, tail-like process, as is also frequently found in allied species. This is still more constant in the newly formed uterine eggs, which measure on an average 0·02 mm., and have usually a very distinct oval form. The tails, which are almost as long as the eggs, always spring from the poles.

Malformations.

There are but few tape-worms which exhibit such frequent and various malformations as *Tænia saginata*. Even the old observers remarked some of them. But as at that time the two species of large-jointed human tape-worms were not clearly distinguished, it would be doubtful whether these observations referred to *T. saginata*

or to Rudolphi's *T. solium*, were it not that the subsidiary circumstances mentioned in almost all cases prove that the reference is to the former. My own observations of such malformations refer almost exclusively to *T. saginata*, as do the researches of Leidy and Welch, which we shall afterwards refer to.[1] Of course, this does not imply that *T. solium* is by any means free from malformations.

Of these different malformations, I will mention first that which consists in the multiplication of the generative openings. This one is by no means rare, and traces of it may be seen in almost every chain. But, as a rule, the multiplication is but inconspicuous, and limited to a few joints. Thus Pallas mentions joints with two or three genital papillæ, sometimes on the same side, sometimes on both sides, in irregular alternation. Nor is this by any means the highest number. I have myself counted five papillæ on one joint, and Colin[2] mentions an unsegmented piece 15 cm. long, which must have possessed at least 25–30 genital pores.

Especially interesting in this connection was a worm sent me by Dr. A. Schmidt of Frankfort on the Main, in which there was a series of such joints in various stages of development. Closer examination showed, however, that the malformation was not confined to an increase in the number of generative openings. Behind each porus genitalis there were the component parts of a perfectly hermaphrodite generative apparatus, as in the normal joints, except that the boundaries of the various organs overlapped a good deal, and that the various parts were not unfrequently imperfectly developed through want of space. This was of course most distinct in the younger unripe joints, where the uteri had not yet attained their full development. When more than two openings are found together in one joint, the sexual organs appertaining to the middle pores are usually the least developed. The uterus is usually shortened, and has few lateral branches, and in the young joints the female germ-producing organs are also small in size. Although the shortening of the uteri is often very marked, and though the stems and various branches of the different systems cross each other abundantly, I have never seen them in direct connection. There were

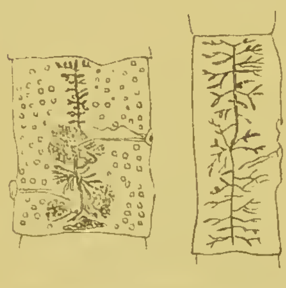


FIG. 257.—Joints of *T. saginata* with two and three genital openings. The first is twice enlarged.

[1] Leidy, *Proc. Acad. Philadelph.*, p. 54, 1871; Welch, *Quart. Journ. Micr. Sci.*, vol. xv., p. 1, 1875.

[2] *Gazette des hôpitaux*, No. 1, 1876.

always as many isolated sets of sexual organs as there were generative openings.[1]

This last fact shows sufficiently that in such cases as the above we have not to deal with joints, as is apparently the case, but with series of joints in which the separation of the individual proglottides has not completely taken place. The slight individualisation which we have already noted as characteristic of some Cestodes, is here present—as an abnormality it is true—in species which usually exhibit a very regular segmentation. Such being the case, we can also understand the great length of the joints with multiplied sexual openings, which may in some cases be as much as 15 cm., as in Colin's piece, but the length of the joints is not usually so great as one might infer from the number of proglottides united, judging by their genital pores. The varying degree in which these openings are approximated gives rise to many differences. A portion of a worm with two genital openings had, for example, a length of 18 mm. instead of about 20, while another with five was only 28 mm. long instead of about 50.

The case is quite different when two genital openings occur in a joint opposite one another on the same level. Here one finds behind each opening a set of male and female ducts, with cirrhus-pouch and vesicula seminalis, but the reproductive organs proper are as usual,—the two vaginæ passing into a common shell-gland, and into a single uterus.

As yet I have seen this malformation only twice[2]—once in a joint which was further abnormal, since the line of demarcation separating it from the preceding joint could only be followed to about the middle.

Such an imperfect separation of neighbouring joints differs really only in degree from fusion, and represents the incipient stage of the latter. This is proved by the fact that the separation is in different cases unequal, the demarcation-line protruding sometimes far into the joint, but sometimes only to a slight distance from the border. A complete absence of the line of demarcation is, of course, a fusion.

FIG. 258.—Double-joint of a *Tænia*, with three sexual openings (nat. size).

As usual, the slighter divergences are by far the more common. This was alluded to in the remark that almost every tape-worm exhibited examples of abnormal individualisation. Sometimes these abnormalities occur repeatedly in the

[1] I have never found the generative openings on the surface as Heller describes and figures in such segments (Art. "Darmschmarotzer," in v. Ziemssen's, "Handb. sp. Path. u. Ther." Bd. vii., p. 601, 1875; transl. "Cyclop. Pract. Med.," vol. vii., p. 716, 1877.

[2] We have already noted (p. 419) that *Tænia vulgaris*, Werner (*T. dentata*, Batsch), is probably in reality a *T. saginata* which has repeatedly undergone this malformation.

same chain, as is the case also with the more marked divergences. Especially interesting in this connection is the specimen observed and drawn by Weinland, whose joints showed, as he says, an unusual "tendency to bifurcation."

I need say little further regarding the structure of the generative organs in these double joints. Each division has of course special genitalia, as a rule quite perfectly developed, though their extremities may perhaps be abnormally approximated. This is even better marked in the case of the undivided side than of the divided, in which, as a rule, the outer border possesses a greater length, and that becomes the more marked the further the dividing line intrudes. In the face of such facts, we cannot close our eyes to the presumption that there is a certain connection between the growth in length and the boundaries of the individual proglottides.

The greater length of the divided side also causes the furrow separating the two parts of such a double joint to incline forwards in a diagonal or curved line. Usually it disappears sooner or later about the middle, but it sometimes happens that it extends to the anterior border. The anterior half then acquires the form of a superfluous joint, and this becomes wedged-in on one side of the chain, between the divergent proglottides, as shown by the first of the annexed figures (Fig. 259, *A*), which is taken from one of Dr. Schmidt's preparations. The inner side of the supernumerary joint was degenerated, as the wedge-like shape suggests. The second figure (*B*) shows a very similar appearance, which was reported to me a long time ago by my late friend and countryman Dr. Krüger of Brunswick.

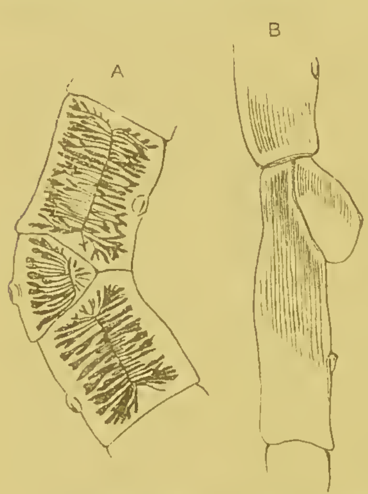


FIG. 259.—Supernumerary joints of *Tænia saginata* (nat. size).

I must, however, leave it undetermined whether the explanation here proposed be the right one or no. Moniez would prefer to deduce the supernumerary wedge-shaped joint from reduplication at the point of proliferation, and would therefore suppose that, instead of one joint, two had formerly arisen beside one another. In the formation of such supernumerary joints he sees the beginning of the double chains of *Tænia marginata* (p. 398), which are distinguished by the fact that the doubling of the point of proliferation persisted for a longer time, and gave rise to a whole supernumerary chain instead of only to a single joint.

I may take this opportunity of mentioning that long since (in 1871) I heard from Dr. Pauli, of Frankfort, of a case which was corroboratory of Moniez's opinion, in so far as it displayed a chain of sexually mature proglottides, one of which bore a lateral chain composed of two long narrow joints. But since the first joint of the main stem was (according to the drawing, for I have not been able to examine the preparation) scarcely broader than the first accessory joint, it is quite possible that the case may be explained by the assumption of a simple division.

With these double structures, the prismatic or triangular chains we have previously mentioned may perhaps be associated. They are, as we know (p. 396), formed from six-rayed heads, and may not unfrequently be observed in *Tænia saginata*. For the first mention of them we are indebted to Bremser,[1] whose specimen is still preserved, according to Diesing, in the Imperial collection of Helminths in Vienna. The worm consisted, according to Bremser, of two chains, which were connected together throughout their entire length by one lateral margin fastened to the other at a sharp angle. We have, unfortunately, no more exact description of the malformation, yet the accompanying figure enables us to see that the two chains must have been at approximately the same stage of development. The common lateral border is projected into a sort of ridge bearing the generative opening. Here and there another pore is present on another border. Levacher[2] has observed a similar monstrosity, only that here the kind of connection was different, in so far as that the one chain was fixed to the other in the middle line. It is doubtful whether the difference represents a real fact, or is not merely verbal, especially since the other cases—the *Tænia lophosoma* of Cobbold, according to Küchenmeister's[3] investigations, the case of Cullingworth and the proglottides sent me by Professor Auerbach of Breslau (Fig. 260)—are all closely related to Bremser's worm. The Hottentot *Tænia*, too, described and figured in the first edition of Küchenmeister's "Parasiten" has also been shown by my investigations to belong to such forms, though the author was at first inclined to regard it as a distinct species (*Tænia*

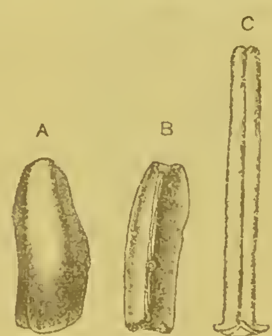


FIG. 260.—Prismatic proglottides (natural size). *A*, From the side; *B*, from in front; *C*, from behind—much extended.

[1] *Loc. cit.*, p. 107, tab. iii., Figs. 12 and 14.

[2] *Institut*, p. 329, 1841. *Comptes rendus*, t. xiii., p. 661, 1841.

[3] "Parasiten," 2d ed., pl. 6, Fig. 6. On Cullingworth's case see *Med. Times and Gaz.*, Dec. 1873. For Cobbold's paper, see *Trans. Pathol. Soc.*, vol. xvii., p. 438, 1866.

from the Cape of Good Hope). It exhibits the same connection between the two chains, except that the one worm has a very much smaller surface than the other, and seems hardly more than a longitudinal ridge, resembling rather the common lateral border of the *Tænia* than the adherent wing.

This longitudinal ridge measured, in the ripe joints which Küchenmeister sent me, only 2 mm., while the adult second wing was about 7 mm. broad. Yet it is the morphological equivalent of a whole animal, as may be inferred, not only from its participation in the segmentation of the worm, but more cogently from the essential similarity of its structure to that of the rest of the body. In thin transverse sections one can see quite distinctly the characteristic cortical and middle layers, both of which pass into the respective layers of the main body.[1] At the free border of the ridge there runs a longitudinal vessel, as also on the free borders of the broad wing; and a third wider one, common to both borders, is situated where the ridge is attached. Outside the vessel the nerve may be observed. As to sexual organs in the ridge, only testes were to be found, and these few in number. Sexual openings were not perceptible there; and even on the free lateral border of the main body none of these could be found; in the preparations examined they were always situated on the common border. In regard to the connection, we must note that the median plane of the ridge forms with the main body an angle of about 45°, which is open externally. Let us imagine the ridge to become broader, or what comes to the same, to become more perfectly developed, then this example would be quite identical with those described by Bremser or Auerbach.

It is, of course, self-evident that, with the uniform development of the two surfaces, the sexual organs will also attain a uniform development. The proglottides sent to me by Auerbach, which were voided by a boy three years old, who had harboured the worm for about one and a half years, have enabled me to obtain a tolerably satisfactory insight into the matter.

First, I would remark that the generative openings, as Auerbach noted in his letters, and as Cobbold and Cullingworth asserted of the worms observed by them, and as is seen in Bremser's figures, are disposed throughout on one side, and are always found on the margin common to the two wings. The alternation which Küchenmeister

[1] Küchenmeister, who has since convinced himself of the fact of this arrangement, appears to have overlooked my observations of twenty years ago, when he, by way of proving that he has succeeded in making out the structure of the tape-worms in question, appeals to his drawings, which "need no patronage whatever from the zoologists," ("Parasiten," 2d ed., preface, p. iv).

reports of his *Tænia* from the Hottentot does not exist; I have reason to believe that the account was based upon error. Nor are supernumerary pores ever observed on the lateral margins of the wings.

The main stem of the uterus runs up the line where the two wings are united to the ridge in a position which we must regard as the morphological axis of the prismatic worm. It has throughout the ordinary structure, and sends out numerous branches towards the three angles, though these are indeed somewhat fewer than usual. The longitudinal ridge which represents the somewhat less developed median wing has the fewest and shortest branches.

But this longitudinal ridge is, as we have noted, the seat of the generative openings, to which the ducts become subsequently connected. I may omit the cirrhus-pouch and its contents; they show as few peculiarities as the generative cloaca. But it is otherwise with the vas deferens, which, after issuing from the cirrhus-pouch, becomes twisted together into a close coil of considerable size, which embraces like a crescent one side of the longitudinal vessel running behind the cirrhus, and then, still coiled, continues to the uterus, from which it bends for some distance backwards. The vagina lies on the same side, but is deeper, and is turned more to the outside. It is difficult to follow it posteriorly, but it is tolerably certain that it gradually changes its original lateral position for a median one, and runs backwards at a short distance behind the longitudinal vessel, between the latter and the coiled vas deferens, or the uterus. The lower end, with the receptaculum and the shell-gland, I have not been able to see distinctly. But the ovary and yolk-gland are present, and their lateral halves belong to the two wings of the triangular joint, and to that aspect which we called the female surface. The longitudinal ridge contains only the median portion of the germ-producing organs. The numerous testes, filled like the vas deferens with semen, are embedded in the interior surfaces of the two wings.

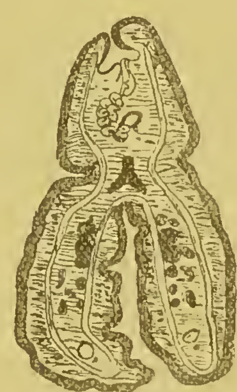


FIG. 261. — Prismatic proglottis in transverse section through the porus genitalis. (× 8.)

Besides the above-described prismatic proglottides, Professor Auerbach also sent me three isolated joints of so strange a structure that a close investigation was required in order to understand them.

On superficial inspection, they appeared as three-cornered depressed cones or hollow pyramids about 8 mm. high, by as many broad. The side walls had also the same size, and were united

together by projecting ridges. At the point where they were fused, at the apex of the pyramid or thereabouts, there were two sexual papillæ generally closely approximated.

At first sight these structures are, as we have said, extremely puzzling, but on closer examination one becomes convinced that they are proglottides in which the prismatic character is combined with a multiplication of the generative papillæ. They represent, in other words, two imperfectly separated prismatic proglottides of asymmetrical arrangement.

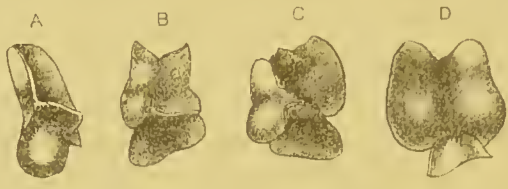


Fig. 262.—Prismatic proglottides with double porus genitalis ; *A*-*C* from the front, *D* (= same specimen as *C*) from behind (nat. size).

The three side walls, although superficially very like one another, are in reality different, since two of them are halves of a symmetrical structure, like the two usual wings, while the third seems to be a wedge-like piece which is intercalated into the triangular space left by the posterior borders of the other two. We may then explain the arrangement of the generative papillæ by supposing that one belongs to the lower end of the longitudinal ridge which runs between the shortened wings, while the other is united to the lower wedge-like portion which is always connected with one of the wings, sometimes with the left and sometimes with the right. The seam between these two parts denotes the anterior border of the wedge-like piece, and the free border of the latter turned towards the other wing is, in spite of its marked contraction, to be regarded as the lateral border. This is in harmony with the fact that the latter bears the second genital papilla high up, close behind the longitudinal ridge. This margin is succeeded by one inclined to it at an angle, and directed somewhat laterally owing to its contraction, but representing the posterior border, as is proved by its projecting and everted margin into which the succeeding joint fits.

Subsequently I found another proglottis which demonstrated the truth of the above representation, inasmuch as it exhibited a stage perfectly intermediate between the ordinary prismatic structure and the one just described. It showed quite undeniably (Fig. 262, *A*) the two ordinary lateral wings and the longitudinal ridge, but differed in that the former were somewhat shorter than usual, and bore the

generative pore far down, and included between them posteriorly a comparatively small and very narrow valve-like wedge.

Although the prismatic form of *Tænia saginata* has been frequently observed, no one has as yet had an opportunity of investigating the head. Yet, from what we know of these malformations, we cannot doubt that these cases are correlated with an unusual structure of the head. As we have already noted (p. 396), it is the six-rayed heads which produce such *monstra per excessum.* The three angles represent the three radii, which are also expressed in the suckers approximated in pairs. Where the ridges are unequally developed, as in Küchenmeister's *Tænia* from the Cape, the position of the suckers is probably also different. Perhaps the suckers belonging to the reduced radius are unusually closely approximated, or are represented by only one, as in the *Tænia* with five suckers observed by Gomez (according to Seeger).

Besides the above malformations, we must also note the forms with perforated joints, the so-called *Tænia fenestrata* (*Ténia percé*). There are tape-worms, some of whose joints are normal, while others are perforated by a larger or smaller hole (Fig. 263). According to Bremser, this results from the rupture of the uterus. The hole is at first small, and always on the upper half of the joint, but sometimes increases to such an extent that the greater part of the worm is destroyed. I have in my possession a piece a foot long, in which the median portion has been wholly destroyed, and in which the joints are held together only by their narrow margins, and thus present the appearance of a rope-ladder (Fig. 263, *B*). A second portion, belonging to another worm, shows, among the 121 joints of which it is composed, all the stages, from the first appearance of the perforation to complete destruction (*A*). What I observe here leads me to doubt whether the plausible explanation of Bremser[1] (who was by no means the first to describe this malformation) be correct. This much at any

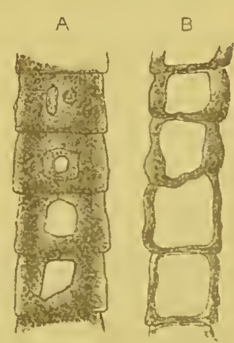


Fig. 263.—Series of joints with perforated proglottides (nat size).

[1] Masars de Cazeles (*Roux Journ.*, t. xxix., p. 26), cited by Bremser, regarded the perforated specimens as representative of a distinct species. The first to observe these phenomena, so far as I know, was Göze, who, on p. 347 of his well-known work, notes that, among the "dentate ('zackengliedrigen') worms" (*i.e.*, *Tænia crassicollis*, auctt.), "there was one with perforated joints. Some joints had in the middle quadrangular holes, with delicate ramifications. The joints themselves were quite contracted and deformed. The worm had probably suffered injury at this point, and was beginning to repair it." Colin (*Gaz. des hôp.*, No. 1, 1876) reports of a patient that some time after the expulsion of *T. fenestrata* normal proglottides again made their appearance.

rate is certain, that the perforation progresses from without inwards, and gradually extends in depth as it increases in breadth. Here and there the hole has two points of origin instead of one, but both are in the anterior half of the joint. The superficial extension is greater anteriorly, so that the posterior wall of the joint is in extreme cases broader than the anterior. This circumstance seems to be in some way associated with the special organization of the sexual apparatus, but this connection can hardly be so simple as Bremser would have it. This is evident enough from the fact that the perforation is sometimes apparent in joints which are still far from maturity.

The true nature of this abnormality—perhaps rather a disease than a malformation—is still unknown. Even Küchenmeister can hardly be right in regarding it merely as the result of digestion. The appearance of the worm, the smooth character of the sides of the holes, and the duration of the malady, are difficult to harmonise with this hypothesis.

The Bladder-Worm of Tænia saginata *and its Development.*

Leuckart, "Die Parasiten des Menschen," Th. i., pp. 296-406 (first edition), 1863.

Having proved that the human intestine harbours not only *Tænia solium*, but a second large-jointed species of *Tænia*, we are naturally led to ask the question, How does this latter originate? Küchenmeister at first (1855) believed that the young of the latter occurred along with the ordinary bladder-worm of the pig, which had meanwhile been experimentally proved to belong to the life-cycle of *Tænia solium*, Rudolphi. In a communication made to the Academy of Paris in 1860,[1] he reports having actually found the young form of *T. saginata* in the pig. The discovery has not, however, been confirmed, and the thrice repeated feeding experiments conducted by Dr. Schmidt in Frankfort and by myself have yielded only a negative result.

But the result of this experiment is not the only argument against Küchenmeister's supposition. The geographical distribution and occurrence of *Tænia saginata* point in another direction.

Specially instructive in this connection is the fact that the Abyssinians, who are almost, without exception, from their earliest years infested with *Tænia saginata*, eat no swine's flesh, but, accord-

[1] *Comptes rendus*, t. l., p. 367. In the second edition of his work on parasites we read (p. 199, note)—"Since my preparation, which I held to be the *Cysticercus* of *T. mediocanellata*, and which was taken from the pig, has been lost, I have no other means of proof. This may be regarded by some as unsatisfactory, but I decline to quarrel over it."

ing to the reports of ancient and modern travellers, and particularly of Davaine in 1860, owe the parasite to their use of the raw flesh of sheep and oxen. This fact of course suggests that one of these animals must be the intermediate host of this *Tænia*, and that the more certainly from the report of the army surgeon Knox,[1] who, during the first Kaffir war in south Africa, witnessed the outbreak of a tape-worm epidemic among the soldiers after they had fed for a lengthened period on "overdriven and unsound" oxen. The South African tape-worm proved from specimens sent me to be really *Tænia saginata*.

To this must be added a statement of Weisse in St. Petersburg,[2] according to whom this common worm not unfrequently occurs in children who have been fed on raw beef for dietetic reasons. This result has been repeatedly confirmed in Germany, and the worm in question is always *T. saginata*, as I first proved from the examination of a case with which I was made acquainted through Dr. Harnier of Cassel. The case mentioned was all the more interesting since it concerned a Jewish child two years of age, belonging to a family in Würzburg, who lived in strict observance of the law.

Guided by these considerations, I determined to experiment on the ox at the earliest opportunity. Huber [3] and Schmidt had already noted the probability of this animal being the intermediate host of *T. saginata*.[4] The latter spoke to me especially of a case where the existence of the parasite could be traced with some certainty to the eating of a meat salad made of raw beef.

The opportunity was soon forthcoming, thanks to the courtesy and sympathy which I have so often experienced from Dr. Schmidt. On the 13th November 1861, when the first edition of my work had been for a long time in the printers' hands, I gave about a yard of some eighty ripe joints of *Tænia saginata* to a calf four weeks old, and eight days later I repeated the feeding with a smaller dose.

The animal experimented on seemed so slightly affected by my experiment, that I was about to extract a muscle, as I was wont to do in such cases, when on the 9th December (*i.e.*, twenty-five and seventeen days after the first and second feedings respectively) my

[1] *Froriep's Notizen*, p. 122, 1822.

[2] *Journal f. Kinderkrankheiten*, Bd. xvi., p. 384, 1857.

[3] *Bericht* xiii. *des naturhist. Vereins, Augsburg*, p. 127, 1860.

[4] Küchenmeister claims priority in this supposition ("Parasiten," 2d ed., p. 149). In the English translation of his text-book (p. 139), published in 1857, he says—"The scolex was either seated in the beef or in mollusks, which might have been in the salad or in the radishes." Apart from the fact that the association of beef and molluscs shows how uncertain was his supposition, it must have been speedily abandoned, for we recall his alleged discovery (in 1860) of the cystic form of *Tænia saginata* in the flesh of the pig.

servant brought me word that it had died during the night. The day before it had been ill and unable to stand, though it had taken its milk as usual.

An immediate *post-mortem* examination showed at once that the feeding had been followed by a rich result. All the muscles, and especially those of the breast and neck, and the psoas, were penetrated by cysts, which had a breadth of 1·5-3 mm., and a length of about 2-4 mm. They were whitish, as if filled with chalky or tubercular masses, such as had never been seen in the young cysts of *Cysticercus cellulosæ.* Inside the exudation layer, which was surrounded by a firm connective-tissue envelope, they contained a clear vesicle of about 0·4-1·7 mm. in diameter. On cutting into the cyst this protruded, and was recognisable as a young *Cysticercus.*

These bladder-worms were round, sometimes pointed at one pole. The internal cavity was small, and mostly confined by the conical vesicle to the distended end of the body. Below the cuticle, which looked as if it were continually shedding off scales, could be distinguished first a thin layer of delicate transverse and longitudinal fibres (the first at intervals of 0·03, the others of 0·05 mm.), whose muscular nature was already evidenced by the powerful contractions of the little worm. Below this there was a thick layer of small cells difficult to isolate, and finally, clothing the internal cavity, large clear vesicles measuring 0·05-0·07 mm. in diameter. Between these there lay yellow balls of irregular and partly ramified appearance. Vessels could not be detected even in the largest bladder-worms, but the latter exhibited already the rudiment of a head, which intruded for about 0·3 mm. into the interior of the very wide bladder cavity, and which seemed to be attached not to the equatorial zone, but to one end of the body. There was as yet no trace of suckers. The interior of the head showed hardly any terminal enlargement, but was in some of the smaller bladder-worms still of a simple conical form.

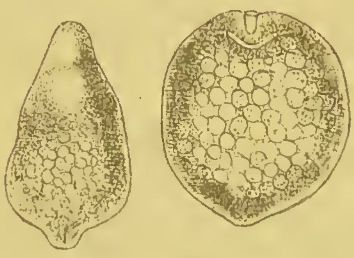


FIG. 264.—Young bladder-worms of *Tænia saginata*, with rudimentary head. (× 30.)

Although these cysts were extremely numerous, and in many places lay so thickly together that their total number must have been many thousands, yet it seemed at first as if the death of the animal under experiment could hardly have been caused by them. It was, however, indeed the *Cysticerci* which had killed the calf. Further examination showed that the distribution of the parasites was in no way confined to the peripheral muscles of the body. The internal

organs were also infested by immense numbers. The muscle of the heart was penetrated throughout its whole extent by larger and smaller cysts, as if with tubercles. The capsule of the kidneys was still more strikingly altered, thousands of little white knots were intercalated between the swollen lymph glands and reddened lymphatics. All these little knots, in spite of their resemblance to tubercles, contained, as we have noted, young *Cysticerci*. This crowd of cysts followed the course of the swollen lymphatic vessels and glands into the inguinal region. The smaller glands, rich in connective tissue, were particularly infested by the cysts, while the larger, although swollen in many cases to the size of a walnut, were almost free from them. The lymphatics of the neck presented a very similar appearance, but somewhat less striking, since there were fewer cysts. Swelling and reddening were always present, so that the whole lymphatic system (with the exception of the thoracic duct) exhibited an abnormal appearance. Some of the glands were not only reddened, but were also full of extravasated blood which penetrated throughout their entire mass. Even under the skin these bloody patches were to be found at various places, and were sometimes as large as beans.

Since the other viscera were comparatively, though not entirely, free from *Cysticerci*—(in the brain I found perhaps a dozen vesicles, lying mostly free between the convolutions of the hemispheres)—I had almost no scruple in referring the death of the animal to the pathological state of the lymphatics. The latter may also be traced to the state of inflammation which resulted from the immigration and development of such a number of parasites.

My respected colleagues, Professor Seitz and Dr. Mosler, to whom I communicated this case, were of exactly the same opinion, and remarked the resemblance between this case and acute miliary tuberculosis.

But whether death resulted from Helminthiasis, or from some accidental complication, the experiment proved this much, that the *Cysticercus* of *Tænia saginata* inhabits the ox, and is developed not only in the muscles, but also in the internal organs, and especially in the lymphatics.[1]

[1] So I concluded in 1861, and so have all my successors concluded, except Küchenmeister, who, in the second edition of his work on Parasites (p. 152), writes as follows:—"Leuckart's first experiment, taken by itself, teaches us nothing, except that, after abundant feeding with the proglottides of *Tænia mediocanellata*, the animal remained long apparently unhurt, till suddenly (twenty-five days after feeding) it died, and exhibited a miliary tuberculosis caused by the Cestode brood. Without the subsequent experiments, I cannot regard the first as of special value in regard to *Tænia mediocanellata*." The accompanying figures will perhaps convince Küchenmeister that the first experiment was of some importance in regard to the *Cysticercus* in question. The results I was able to draw from that case are still almost the only ones forthcoming on this point.

From the character of the bladders one could not help noticing that they represented the early stages of a new *Cysticercus*, different from the *Cysticercus cellulosæ* of the pig.

A second feeding experiment, which I began on the 27th December, enabled me to supplement the results of the first.

Remembering the fatal issue of the former case, I used smaller doses. First I gave twenty-five proglottides, and then several doses of from five to eight at intervals of five or six days. After between forty and fifty joints had thus been administered from two tape-worms, voided soon after one another, the feeding process ceased. Twenty days after the first infection many pathological phenomena (loss of appetite, fatigue, ruffling of the hair, and fever) appeared, which gradually increased to such an extent that I was for a while afraid that the animal would not survive. Towards the middle of the second week the disease diminished, till finally perfect health returned.

Forty-eight days after the first, and thirty after the last feeding, I extracted the sterno-mastoid muscle of the left side. Even during the operation I observed, to my joy, the *Cysticerci* embedded among the fibres. They had a somewhat oblong shape, and varied from 3 to 5 mm. in their longest diameter. Their appearance was still somewhat dull, but I saw the worm glimmering through the walls. It was generally situated in the middle, whilst the ends of the cysts were completely filled by the abundant granular cells and exudation-granules.

In the extracted muscle I counted perhaps a dozen cysts, among which there were some with wrinkled walls, and dead or disintegrated inmates.

The worms without their shells measured between 2 and 3·6 mm. in their longest diameter. The smaller specimens were almost all spherical, while the larger already possessed a distinctly oblong form, with diameters of 3·6 and 2 mm. Otherwise these parasites were like the young tape-worms of the pig of the same age, and this to such a degree that, without knowing the circumstances and without close examination, the two forms might easily have been confused. In regard to the point where the head is fixed there is at this period no difference, since the head springs from the equatorial zone, instead of from the end of the body, and is seen as a white opacity in the otherwise translucent wall of the bladder. The previously divergent situation of the head suggests an inference as to the phenomena of growth in the bladder-worms of the muscles, and justifies the statement that their longest diameter is by no means morphologically identical with the long diameter of the other bladder-worms.

The rudimentary head of the smallest bladder-worms appeared, on close inspection, as a short cylinder 0·35 mm. across, and 0·6 mm. long. The receptacle was always in close contact with the outer surface. The sharp bend which is prominent in the *Cysticercus cellulosæ* at a still earlier stage (p. 348) is not to be seen here, although the cavity of the head is already considerably expanded at the lower end, and the narrow neck is not unfrequently contracted into a coil. I was struck by the presence of numerous small granules (0·007 mm.) which filled the greater part of the cavity of the head (Fig. 265), and by their firmness, resistance to chemical reagents, and optical characters, reminded me forcibly of the chitinous balls observed in the male genital pouches of the young stages of *Pentastomum.*[1] The entrance into the head-cavity formed a transverse slit, which crossed the longest diameter of the body of the bladder-worm at right angles. Round about this slit several small calcareous bodies were to be seen. The wall of the bladder was penetrated by a rich vascular network, some branches of which passed into the insertion of the head, and were continued into the substance of the latter.

FIG. 265. — Head-rudiment of *Cysticercus Tæniæ saginatæ* before the development of the suckers. (× 25.)

FIG. 266. — Head-rudiment of *Cysticercus Tæniæ saginatæ* after development of the suckers. (× 25.)

The larger bladder-worms of the extracted muscle were manifestly older phases of the above. Their head-rudiment had grown with the body to a size of 0·8–1 mm. The lower portion of the head-cavity had enlarged to a spherical space of almost 0·5 mm. in diameter. The pockets for the suckers were formed, and were almost all clad with their muscular sheaths, though the disposition of the head was essentially the same as before (Fig. 266).

What struck me most in regard to these bladder-worms was the fact that they, although the descendants and young forms of a hookless tape-worm, were furnished with a distinct though small rostellum, and with the rudiments of hooks. This was all the more striking,

[1] Leuckart, "Bau und Entwickelungsgesch. d. Pentastomen," p. 140 : Leipzig, 1860.

since the occurrence of these structures in the adult tape-worms was at that time all but unknown, for it was the prevailing opinion that the complete absence of these structures was one of the most important characters of *Tænia saginata.* We have since learned that this is not the case, and the above observation has thus lost much of its former importance. But it is still of sufficient interest to claim our attention here.

The structure just mentioned consisted of a pit-like depression, or of a diverticulum from the head-cavity. It lay between the suckers, and therefore belonged to the apical surface. It reminded one much of the cavity of a sucker, especially since it was similarly ensheathed by a muscular layer, and was of almost the same size (0·25 mm.). There could be no doubt as to its nature; it was a rostellum, a structure therefore which afterwards remains abortive when compared with the suckers, and is thus not to be found without difficulty in the adult.

The anterior border of the apical pouch did not pass directly into the cavity of the head, but was separated from it by an annular diaphragm—a structure which occurs at first in exactly the same way in the hook-bearing bladder-worms (p. 351), but passes in the latter forms ultimately into the apical lid ("Scheiteldecke"), into which the basal roots of the hooks are fixed. The resemblance was all the more striking since the border of the diaphragm was furnished with a close circle of small points (0·0035 mm.), just like those at first found in the situation of the subsequent hooks in the armed forms. Here and there these points were also present, deep down in the apical cavity or in the suckers.

If the structure of this organ were not the same in all bladder-worms (even in those with perfectly formed suckers), one might suppose that a subsequent development into the ordinary structure of the hook-bearing forms took place. The facts of the case, however, only admit this hypothesis on the presumption that the chronological order of the developmental processes in *Tænia saginata* is different from that observed in the other cystic tape-worms, in which, by the time the suckers are fully developed, the metamorphosis of the hooks and apical plate is also almost complete. But such a presumption was not in any way justified by the condition of the adult *Tænia.*

The calf experimented upon furnished material for definitely investigating the development of this structure. This examination was necessarily deferred for a time, so that the result might be indisputable. I therefore postponed the investigation for seven weeks, until the bladder-worm might be reasonably supposed to have attained maturity. One bladder-worm, which I cut out during this period because it was visible through the skin of the under surface of the

tongue, and was therefore easily accessible, exhibited hardly any noteworthy change.

The appearance of the muscle three months after feeding was exceedingly like that of measly pork. Oblong vesicles, with large nuclei, were to be seen in great numbers, especially in the anterior half of the trunk between the muscle-fibres (Fig. 267). Their length varied from 4 to 8 mm., while their breadth was somewhat uniformly 3 mm. The head-rudiment had very considerably increased in size, and formed a rounded appendage 1 to 1·3 mm. long by 0·7 to 0·9 mm. broad. The organization of the head was, however, still unaltered. Instead of a rostellum armed with hooks, the previous structure was still present, except that the points had now disappeared on most of the specimens. The neck not only contained a large number of calcareous bodies, but was also much longer than before, and had contracted into numerous close folds within the receptacle (Fig. 268). At first very small when compared with the head, it now appeared as by far the most conspicuous portion of the whole mass. The head was confined to the lower end, and was not unfrequently much contracted longitudinally, and displaced to one side, exhibiting many irregularities in form and position.

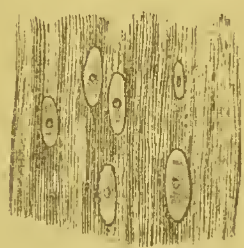


FIG. 267.—*Cysticercus Tæniæ saginatæ*, embedded in the muscle (nat. size).

FIG. 268.—Head-rudiment of an adult *Cysticercus*. (× 12.)

FIG. 269.—*Cysticercus* with evaginated head. (× 3.)

The structure of the parasite becomes most evident when a longitudinal section is taken through the head, or when it is protruded by intentional pressure. In the latter case one notices at once a wrinkled appendage about 3 or 4 mm. long, which has a somewhat opaque appearance, due to the thickness of its walls and the abundance of its calcareous corpuscles, and which runs forwards to the head and the suckers. The latter organs have not yet attained their full size, since they measure at most 0·35 to 0·4 mm., but they are markedly larger than the suckers of *Cysticercus cellulosæ* of the same age. On the apex the head bears an opening about 0·14 mm. in diameter, which leads into the cavity already mentioned, and, with the rostellum just beneath, is to be regarded as a sort of frontal sucker, such as we

have found in still more distinct form in other hookless Tæniadæ (Fig. 271). The size of this apparatus is hardly changed, so that it is

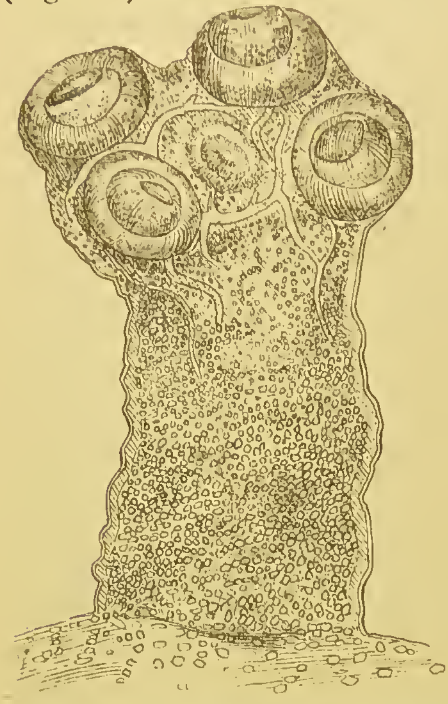


FIG. 270.—Evaginated head of *Cysticercus Tæniæ saginatæ.* (× 30.)

FIG. 271.—Longitudinal section through the head *in situ.* (× 30.)

now much smaller than the lateral cups to which it was formerly equal. Round about the rostellum one notices as usual a vascular ring, into which the four longitudinal vessels open (Fig. 270). Even the lateral branches of the latter can sometimes be followed for some distance.

As to the distribution of the bladder-worms in the body of the calf, I may remark that the large majority were found in the muscles. After the muscles of the breast and neck those of the heart were most infested, and specially those of the right ventricle. But the greater number of the bladder-worms in the heart had perished before their full development, as was evident from the dirty white tubercular little masses (1-3 mm.) which shone through the serous lining. Similar deposits were found in many other organs, especially in the liver and the lungs, which also exhibited some adult bladder-worms. Similarly in the thymus gland, the capsule of the kidney, and in the brain.

The lymphatic system was quite normal, but in the inguinal region, in Douglas' space and in other situations, numerous bluish-red bodies, about the size of a pea and less, were to be noted, as in the first animal. At many places the intestines were somewhat adherent to one another, and also to the peritoneal lining of the body-cavity,

phenomena which clearly indicated an inflammatory state, appearing as the result of the experiment.

I also succeeded in bringing the bladder-worms of *Tænia saginata* to development in the calf, and in watching the various stages up to complete maturity. The hitherto often disputed distinctness of the species was undeniably established, and one of the most important sources of human food—the ox—was shown to be the intermediate host of the most frequent and most widely distributed tape-worm. At the same time it was experimentally established that the abundant importation of tape-worm eggs containing embryos into the ox occasioned a dangerous, and, under some circumstances, fatal disease, which might, on anatomical grounds, be justly designated "acute cestode tuberculosis."

Considering the enormous import of these facts to Helminthology, hygiene, and pathology alike, it is not surprising that my experiment was abundantly repeated by helminthologists, physicians, and especially by veterinarians. Similar investigations have been made on several animals by Mosler (1864), Röll (1865), Gerlach (1869), Zürn (1871), Zenker (1872), Probstmayr (1879), and in England by Simonds and Cobbold (1865 and 1866), in Belgium by the younger van Beneden (1879), in France by St. Cyr (1873), as well as by Masse and Pourquier (1877), and in Italy by Perroncito (1877).

With very few exceptions, these experiments yielded a positive result. The exceptions include only an experiment made by Simonds and Cobbold,[1] and a double experiment made by Küchenmeister, Haubner, and Leisering, which I do not count, since the maturity of the proglottides was not ascertained, and since they were, in one case at least, decidedly unripe. The calves or oxen under experiment all became diseased with more or less striking, and often fatal, symptoms, and exhibited on dissection numerous bladder-worms in the muscles, and often in the viscera. These represented the results of the feeding at various stages of development, but many of them were frequently dead. They numbered usually many thousands, and in one case where they had all perished at an early stage of development, they were estimated by Simonds and Cobbold at about twelve millions. In this case, indeed, about four hundred proglottides had been given to the animal within two months, which had, however, in spite of their number, only a comparatively slight illness.[2]

[1] Küchenmeister is mistaken in saying that Gerlach's experiment was without result ("Parasiten," second edition, p. 153). See *Bericht d. Thierarzneisch. Hannover*, p. 70, 1869, where it is expressly noted that the calf, which was killed five months after feeding, was "penetrated through and through with bladder-worms."

[2] *Journ. Linn. Soc.* (Zool.), vol. ix., pp. 170, 1868.

The very reverse of this experiment is furnished by Zenker's case,[1] in which a calf was fed with only a single proglottis—whether full of eggs or not is doubtful—and remained in perfect health, yielding only three bladder-worms in the muscles of the back.

To our knowledge of the structure and development of this bladder-worm all these observations have added but little. As far as anatomical facts are concerned, they simply corroborate my former statements. Only one point has been made clearer, and that by Ed. van Beneden, who, as was formerly remarked (p. 360), was fortunate enough[2] to observe numerous young *Cysticerci* still retaining their embryonic hooks twenty-one days after feeding. In three cases he was able to find all the six hooks, while in other cases only one or a few were to be seen. A sketch he was kind enough to send me shows the six hooks at some distance from one another, but yet still approximated in pairs, and at their original place of insertion by the side of the rudimentary head, which had reached the stage shown in Fig. 264. In form, size, and histological structure, the young bladder-worms had the greatest resemblance to the worms first observed by me. Calcareous corpuscles and vessels were still absent. The heads in many specimens were still indistinct, or in process of development. Their place of formation did not appear quite constant, seeming sometimes to lie somewhat laterally instead of in the longitudinal axis of the bladder.

We have, however, to thank the above investigators for important results as to the pathological influence of these parasites. The memoirs of Mosler,[3] Zürn,[4] Simonds and Cobbold, and van Beneden, are specially worthy of mention, because they have elucidated many points with respect to the nature of acute cestode tuberculosis.

Zürn's case has been perhaps most accurately followed in its pathological bearings. A calf three months old, which had been fed with fifty-seven ripe proglottides, exhibited symptoms of disease on the fourth day after infection. The animal had a high temperature (40° C., instead of 39·2°) and a somewhat raised pulse, ate little, and had an inflated belly, which was sensitive to touch. These symptoms were probably caused by the wandering of the embryos, as is shown by the fact that they disappeared after a short time, with the exception of pain which seemed to be felt when the walls of the belly were pressed. A slight fever (with a temperature of 40·3°) also per-

[1] *Sitzungsb. d. phys. med. Gesellsch. Erlangen*, Heft iv., pp. 71, 87, 1872.

[2] The investigations referred to were communicated to me in manuscript by my esteemed friend, and have since been published, *Bull. Acad. Sci. Belgique*, t. xlix., p. 659, 1880.

[3] "Helminthologische Studien und Beobachtungen," pp. 1-22: Berlin, 1864.

[4] "Arbeiten der landwirthschaftl. Versuchsstation Jena," *Zeitschr. f. Parasitenkunde*, Bd. i., p. 363, 1869.

sisted. The other symptoms returned in greater intensity five days later, *i.e.*, nine after the feeding. From that time the fever increased, until, on the seventeenth day, the temperature in the rectum reached 41·8°, the appetite also failed, the animal became feeble and declined, lay much, and moved only with difficulty and pain. At last it could hardly move without help, and was attacked by diarrhœa. On the eighteenth day the temperature again began to fall. The animal was quite unable to raise itself, the heart's action became gradually slower, the respiration laboured, and four days later death ensued from failure of the heart's action.

The results of *post mortem* examination are essentially the same according to all investigators. The subcuticular connective tissue, in many places, and especially where there are large lymph-glands, is infiltrated by a serous fluid of a briny character. The muscles are of a deep red colour, markedly injected, and in many places also exhibit streaky exudations. They are further of a succulent consistency, and are softened here and there, and penetrated by numerous cysts,[1] especially in the tongue, throat, neck, and breast. The heart is no exception to this, but is often even more infested than the other muscles, not only in its walls, but in its papillæ and valves, and below the endocardium. The circumference and bulk of the heart are considerably increased. The same is true of the kidneys, and to a less extent also of the liver. The viscera (with the exception of the genitalia) are congested, the peritoneum is reddened, the lymphatics much distended, the glands enlarged, and also to some extent altered by extravasation of blood. The peritoneal and pleural cavities contain a serous fluid. The membranes of the brain are very hyperæmic, and the lateral ventricles distended, while the brain substance and the pia mater exhibit a few extravasations.

The extent of the occurrence and distribution of the bladder-worms in the internal organs varies greatly, and is sometimes only slight, although the peritoneum and lymphatic apparatus are seldom quite free from them. The kidneys, lungs, and liver contain on the whole but few. Mosler saw some bladder-worms in the muscular layer of the intestine, Perroncito[2] in the brain, and van Beneden in the subcuticular connective tissue, and one example even in the vitreous body of the eye, which lay in the centre of a bloody granular mass, some millimetres in front of the retina.

The pathological changes which we have described vary, of course,

[1] Van Beneden finds in these cysts, besides the granules and granular cells which I mentioned, numerous free blood corpuscles.

[2] "Esperimenti sulla produzione del Cysticercus della Tænia mediocanellata," p. 11 : Torino, 1877.

greatly according to the intensity of the attack. The disease may, indeed, assume another and perhaps less dangerous character. In slight cases it is confined to insignificant and almost non-febrile disorders of the digestive and locomotor functions. The animals lose their appetite and liveliness, and grow thin, but in about two months, according to Gerlach's case, or even sooner, according to Simonds and Cobbold, return to the normal condition. If the disease attain full development, it has, not only anatomically, but in its external symptoms, an unmistakeable resemblance to miliary tuberculosis, which results in a sort of typhoid fever.

In regard to the cause of death of the animals, very different hypotheses have been advanced. I have expressed the opinion that it is to be found in the derangement of the lymphatic system. This was very pronounced in the first of my cases, and might perhaps be referred to the irritation produced by the parasites which had migrated into the lymphatics, and had there developed in large numbers. Although this affection is, as a matter of fact, to be regarded as a constant sign of acute miliary tuberculosis, Mosler thinks my explanation must be rejected. He is of the opinion that death is due to the changes occurring in the heart, which entail disturbances of the circulation and associated dropsical exudations. And lastly, van Beneden regards the death of the animal as the result of a whole series of pathological processes. Besides the well-known alterations in the muscles, connective tissue, and heart, he finds signs of peritonitis, and observes clots of blood, not only in the right ventricle and in the left auricle, but also at the bifurcation of the pulmonary artery, in the posterior end of the aorta, and in the circle of Willis. These clots completely close some of the vessels in question, and help to explain how, in the final stages of the disorder, the posterior extremities of the animal become paralysed and insensible. Although a bladder-worm has only once been found in these thrombi, and then in the interior of one in the heart, van Beneden thinks that they are in all cases to be referred to parasites which have, somehow or other, passed into the vascular apparatus, perhaps from the pericardium. He even thinks it possible that the numerous extravasations of blood found in the animal had been caused by migrating worms, and finally expresses the conviction that the embryos pass into the blood-vessels at an early stage, and are distributed throughout the body along with the blood.

But, however the question as to the cause of death may be settled, this much is certain, that *it is the ox that harbours the bladder-worm of* Tænia saginata, *and conveys it to us in its flesh.*

In view of this fact, it is further very surprising that the bladder-worm from the ox, which cannot be very rare, from the frequency

of the associated tape-worm, only became known when its existence was proved by my experiments. This is explained, however, when we take into account the habits of the ox, and consider that it is not only kept clean and carefully tended, but that, being entirely a herbivorous animal, it has seldom opportunity to swallow large masses of worms with the food which it takes in the open air. It will, therefore, usually pick up only single proglottides, and, as we learn from the result of Zenker's experiment, this would furnish, as a rule, only few bladder-worms. The parasites are, moreover, distributed over a large mass of flesh, so that they only occur separately, and may be all the more easily overlooked, since, even in their adult state, they are hardly ever larger than a pea.

But even since the discovery of the bladder-worms they have but rarely come within the range of observation, at least in Germany and the neighbouring countries. Siedamgrotzky once found one in Zurich, in the muscle of the lip of a living ox;[1] and Closs, in Frankfort, proved its presence in a tongue, which (according to Heller) is still preserved, partly in the collection of the Senkenberg Institute, and partly in the Pathological Institution at Kiel. Guillebeau[2] has also lately found another instance of the occurrence of the bladder-worm in the tongue of an ox.

In other districts, bladder-worms from the muscle of the ox have been more frequently observed. We learn, for example, from Knoch[3] that the St. Petersburg sausage manufacturers have long known them, and that they describe them, in contrast to the pig bladder-worms, as "dry, hard, and not so watery"—a description which is in complete harmony with the smaller size of the bladder, and the accumulation of the "cheesy" enveloping substance. Knoch himself first observed the bladder-worms in a cutlet, which came to table cooked, and it was afterwards established, by his investigations, that the flesh of the cow in question, which came from the neighbourhood of St. Petersburg, was everywhere infested with cysts "of a dirty white colour, or inclining to yellow."[4] According to the assurance of the vendor, the newly cut meat had been inspected by the police medical inspector, and pronounced faultless. As we are informed in the description, the bladder-worms were, moreover, in very different stages; for while some were quite full grown, others had not even the rudiments of a head, so that we are justified in concluding that there had been a repeated

[1] *Bericht d. naturf. Gesellsch. zu Zurich*, Dec. 1869.

[2] *Mitth. nat. Gesellsch. Bern*, p. 21, 1879.

[3] *St. Petersburg Medical Gazette*, vol. x., p. 245, 1866 (Russian.)

[4] *Bull. Acad. impér. St. Petersbourg*, t. xii., p. 347, 1867. While attempting to give these opinions prominence rather than my own, I must say that there are many statements and representations in the course of the essay which I am forced to reject.

and long-continued infection. The host of the adult tape-worm had probably lived somewhere in the near neighbourhood of the cow.

In Algiers, where *Tænia saginata* is very prevalent among Jews, Mohammedans, and Christians,[1] the bladder-worm was repeatedly observed by Chauvel in the diaphragm, and by Arnould in the loins. This was also the case in Beyrout, where Talairach, a French naval surgeon, found bladder-worms in the meat supply after a large per-centage of the crew had become infected by eating beefsteak *à l'Anglaise.*[2]

The frequency of the occurrence of the bladder-worm is of course always determined by the conditions of infection, and these vary not only according to the local circumstances and the abundance of the tape-worm, but also according to the customs of the inhabitants and their relations to the animal. This explains what has been lately reported of the very wide distribution and extraordinary numbers of this bladder-worm in Abyssinia and India, especially in the Punjaub, where all these conditions are present. The most comprehensive statements regarding this are those of the English physicians in India, and especially Fleming and Lewis,[3] whose communications have become widely known, owing to their publication in the English Medical Journals,[4] and to Cobbold's summary of them.[5] As above mentioned, the bladder-worm is especially common in the Punjaub, where in 1869 not less than 768 out of 13,800 cattle were infected (Cunningham), while in the previous year the per-centage was even greater (6·12 per cent. instead of 5·5). Fleming mentions that during the six years of his service there he hardly ever saw an ox or a cow that was not infected with bladder-worms, although they were not always confined to the muscles. Nor were they only found separately, but sometimes in such numbers that Lewis counted in a pound of flesh no fewer than 300 living *Cysticerci.* The flesh was taken from the psoas muscle, for which and for the glutei the bladder-worms seem, according to the Indian experience, to have a special preference. The parasites were also often gathered together in larger or smaller numbers at the root of the tongue, in which position some of them attained a length of almost an inch.

This very frequent occurrence is accounted for when we learn from the above-mentioned sources that the Indian oxen are not nearly

1 *Ann. d. sci. nat.*, t. xvii., Art. 15, 1873.
2 *Mém. Acad. méd.*, p. 998: Paris, 1877.
3 The original papers are to be found chiefly in the *Indian Medical Gazette*, 1869, in the *Bombay Health Officer's Report*, 1870, and in the *Madras Monthly Journ. Med. Sci.*, 1873.
4 *The Lancet*, p. 860, 1872; *The Veterinarian*, p. 484, 1873.
5 "The Internal Parasites of our Domestic Animals," Chaps. iii., iv., v.: London, 1874.

so exclusive in the choice of their food as our European horned cattle, which are better kept and in cleaner stalls. Fleming has himself seen oxen and sheep, as well as pigs, devouring human excreta with great satisfaction. As the principal seats of the infection he rightly regards the dirty pools and sloughs in the neighbourhood of the Indian villages, where the manure of the district is collected, and along with it the eggs and joints of the universally distributed tape-worms. These are afterwards still more dispersed by the rain, and carried into the cisterns,[1] the contents of which are always polluted with excreta, so that the animals are infected by drinking as well as by grazing.

The frequency and distribution of the bladder-worms from the ox in Abyssinia seems to be due to very similar circumstances. This I learn from a communication from Schimper to Al. Braun, which lies before me in the original, but which, so far as I know, has not yet been published. The bladder-worms are, he says, really forced upon the ox by a very blameworthy practice of the inhabitants. The Abyssinians, he continues, ease themselves in the open air, not far from their dwellings, and indeed regularly at daybreak, in the early grey of morning. At this time whole companies of them may be seen daily cowering upon the ground in conversation. Their clothing, which is like a white bed-cover, envelops the whole body from the shoulders downwards, and also covers the spot on which they sit. One thus perceives nothing of what is really taking place, but only sees people cowering down at some distance from each other and talking. To a stranger it seems very surprising that every day a company should assemble to talk at such an unusual hour in the open air, and in the cold and damp of the morning; the real business is still hidden from him; and even afterwards he finds it difficult to understand how the Abyssinians find it pleasanter to do in company and for quarter of an hour what others do hurriedly and in secret. After this matter is accomplished, the cattle are let out of the shed. But they have to remain in the neighbourhood until the bread for the herdsmen is baked and eaten. Only then are they driven off to pasture. Meanwhile they remain in a place in which millions of tape-worm eggs have just been deposited, many of which have of course been transferred to grass and herbs and loose straw. The cattle, eating these substances, swallow the eggs along with them, and afterwards become infected with bladder-worms.

I must, however, expressly mention that Schimper had no knowledge of the investigations instituted in Europe regarding the con-

[1] Dr. Oliver has also distinctly proved by microscopic investigation the presence of tape-worm eggs in the cistern-water of the Punjaub.

nection of *Tænia saginata* with the bladder-worm of the ox, nor had he observed bladder-worms in the muscles of cattle. If, notwithstanding this, he connects man and the ox in the way indicated, he is supported not by the observations mentioned, but chiefly by the fact that of all the domestic animals the ox holds by far the most important place in the food of the Abyssinians. As pigs are never reared nor eaten, only the sheep and the goat can be taken into account besides the ox. But Schimper always found the goat free from bladder-worms, although harbouring a tape-worm "whose proglottides are similar to those found in man, and often occur in immense numbers in the excreta." The sheep, it is true, is often infested in Abyssinia by bladder-worms, but only in the liver (and in the hilly country also in the brain); but these hepatic bladder-worms, which it is casually remarked are longer than those found in the ox, and have "on the two opposite sides a slender, membranous, wing-like structure," cannot produce the human tape-worm, since the liver is not eaten, but thrown away. On the other hand, Schimper thinks it very likely that the tape-worm of the goat just mentioned is derived from these sheep bladder-worms, especially as this animal might very easily become infected with them.

Although Schimper expressly states that he always found the goat free from bladder-worms in the muscles, and although two experiments made by Zürn and myself on this animal produced no positive results, Zenker has succeeded in rearing[1] the bladder-worm of *Tænia saginata* in the goat. Twelve weeks after the feeding, Zenker found (besides numerous compressed cheesy and calcareous bladder-worms in the capsule of the kidney, liver, lungs, brain, heart, and muscles) two fully developed living bladder-worms, regarding whose origin there could be no doubt. On the other hand, however, these scanty results serve to prove that the goat is but little adapted for the breeding of the tape-worm.

All attempts to breed the parasites in other animals have failed. Mosler, Cobbold, Zenker, and van Beneden experimented on the pig just as unsuccessfully as Schmidt and I formerly did. Zürn fed a sheep[2] with *Tænia saginata*, but it remained healthy and free from bladder-worms, as I had formerly observed. In my case the animal had devoured about sixty ripe proglottides, and on *post mortem* examination eight weeks later, the only alteration observed was the presence of many small white dots in the liver, and a shrunken appearance of the lymphatic glands of the groin and pelvis, which were

[1] *Loc. cit.*, p. 88, 1872.

[2] The muscle bladder-worms which are now and then found in the sheep possess hooks, and thus cannot belong to *Tænia saginata*.

also much infiltrated with blood. The same negative experiment was made by Masse and Pourquier,[1] not only on lambs and sheep, but on a rabbit and a dog. It was also made by Probstmayr[2] on a dog, and by Heller [3] on rabbits, guinea-pigs, and apes.

The only animal, besides the ox and Zenker's goat, which has hitherto exhibited the bladder-worm of *Tænia saginata* is the giraffe—not the gazelle, as Küchenmeister asserts. Moebius found in the flesh of one of these animals, in the zoological garden at Hamburg, abundant specimens of this species.[4] It is very likely that the animal had been infected in its home in the same way as the Abyssinian oxen.

From the danger which attends the migration and development of these bladder-worms, we may regard it as a very fortunate circumstance that man is exempt from them. It is true that Heller[5] lately stated that Colberg in Kiel identified a human bladder-worm (from the eye) as the *Cysticercus Tæniæ saginatæ*, but, so far as I know, no further details have been published on this point. So that until the connection of the animal with the tape-worm is established by more explicit statements, I think I am at liberty to doubt the correctness of the diagnosis, especially as it is well known that there are bladder-worms of *Tænia solium* with stunted or even quite abortive hooks. So much at least is certain, that if the bladder-worms of *Tænia saginata* were at all capable of development in man, many of them would be found in the almost countless cases in which *Cysticerci* occur in the brain and in the muscles. Their occurrence would probably be even more frequent, since the risk of infection is much greater with the constantly spontaneously liberated proglottides of *Tænia saginata* than in the case of *T. solium.*

How long the bladder-worm of *T. saginata* remains living in its host cannot at present be decided. But we may reckon the length of its stay there at several years, judging from its great resemblance in occurrence, nature, and time of development to the ordinary bladder-worm of the pig. The fact that the bladder-worms of *T. saginata* (perhaps in connection with the lively reactions which they call forth on the part of the host) are destroyed much more frequently and in much greater numbers while young, than is the case with the bladder-worms of the pig, can hardly allow any inference as to the fate of the survivors. Besides this, it appears as though it were principally the bladder-worms in the viscera which are liable to this destruction.

[1] *Ann. méd. vétér. Bruxelles*, 1876.

[2] *Jahrb. der Münchner Thierarzneischule*, 1869-70.

[3] *Loc. cit.*, Bd. vii., p. 602, 1875 (English transl., vol. vii., p. 718).

[4] *Zoologischer Garten*, Bd. xii., p. 168, 1876.

[5] *Loc. cit.*, Bd. iii., p. 294 (Engl. transl., vol. iii., p. 556).

Occurrence and Medicinal Significance of Tænia saginata.

Tænia saginata belongs, like *Ascaris lumbricoides* and *Oxyuris vermicularis*, to the cosmopolitan parasites. It is found wherever the ox is domesticated, and wherever its flesh forms an important or prominent article of food. The frequency of the tape-worm, of course, varies very much according to the countries and districts in which it is found. It depends upon the presence of the bladder-worm, and thus ultimately upon the keeping and care of the ox, as well as on the preparation of the flesh. In places where this is done without sufficient care, and the flesh is eaten perhaps in a half-cooked or raw condition, the tape-worm is naturally of very common occurrence. If, in addition to this custom, the cattle be negligently tended, and if uncleanliness prevail in the stable yard and house, it is easy to understand that both young and old, it matters not of what sex or station in life, will be infested by these parasites.

Thus it was mentioned by Bruce, more than a century ago, that the Abyssinians, whose morning occupation Schimper has so realistically described, eat raw flesh, and are consequently almost all infected with tape-worm, and, as has already been noted, with *Tænia saginata.*[1] Exceptions are extremely rare; the worm appears even in children of three or four, as soon as they begin, like their parents, to eat the flesh "fresh and raw, and, if possible, still warm and quivering" (Schimper). Even the Mohammedans and Europeans, who scorn to live *à l'Abyssinienne*, are not entirely exempt from parasites, although they are, of course, less exposed to them. Schimper himself was attacked by them eight years after his settlement abroad. The bladder-worms, or their heads, are distributed everywhere by the universally prevailing uncleanliness, and the almost gipsy-like mode of life of the inhabitants. Schimper conjectures that they are sometimes carried by flies. They adhere to table utensils—to knives, spoons, and plates—and thus opportunities of infection are everywhere afforded. And their distribution takes place all the more easily since there are no sanitary commissions, no slaughter-houses, and no butchers, but every one who wishes to eat flesh must kill the animal upon his own premises. Only from "a radical change in the degraded social condition" does Schimper hope for any improvement.

Further, the Abyssinians do not regard the tape-worm as entirely an evil. They maintain, on the contrary, and Schimper agrees with them from his own experience, that without this guest they would be

[1] This we learn not only from the descriptions given by Bilharz (*Zeitschr. d. Gesellsch. d. Aerzte in Wien*, I., No. 28, 1858), and by Schimper (*in litt.*), but from the investigations which Küchenmeister made upon specimens sent by the former.

unhealthy, and that they would suffer especially from constipation and its consequences. When the tape-worm is present, the stools are somewhat fluid and uniform, thus imparting a greater power of resistance against the rapid changes of temperature which prevail in a mountainous country, and also decreasing the tendency to disease, especially of an inflammatory nature. For this reason the Abyssinians use cousso, not to expel the worm, which, in fact, it rarely does, but only to shorten its length. As a rule they take, as Schimper remarks, a dose every two months, which at these intervals, has only the effect of not allowing the worm to become so long as to be troublesome to its host. The time at which it reaches this stage varies, however, according to the diet of the individual. Those who take little but good food are not troubled by the size of the worm for a long time; while others, and especially those who eat raw flesh in excess, are afflicted by a remarkably rapid growth of the parasite. When the worm is from 12 to 24 feet long, the expulsion of the proglottides begins (Schimper), and from eight to twelve of them come away daily. Now and then a pause occurs for some days, although it may be assumed that the chain lengthens at the rate of 8 to 12 inches[1] in twenty-four hours. If the growth and expulsion be proportionate, the worm excites no uneasiness; but, as a rule, the former preponderates, and thus it happens that the worm becomes longer with age. It must not, however, be immediately concluded that there is an insufficient expulsion merely because only a small number of joints, or none at all, are separated; for the separated joints often remain in the intestine in larger or smaller numbers, until they perish and disappear, and are ultimately voided in an unrecognisable condition along with the excreta.

Abyssinia is, moreover, not the only country in Africa in which *Tænia saginata* occurs. We know that it is also found in Nubia, Ethiopia, the Cape, Senegambia, Algiers, and Egypt. Thus it seems to be pretty well distributed over the whole of Africa, and in many of these countries is extremely frequent, though not so common, as in Abyssinia. According to Pruner, one can hardly open the body of a negro without finding *Tænia lata* (according to Bilharz, our *T. saginata*).

In Asia we find a similar distribution and frequency. From the above-mentioned reports of the English army surgeons, there can be no doubt as to its occurrence in India, although no express mention is made of it. It is particularly the Mussulman population of the Punjaub that suffers from it, and especially in the lower classes, who

[1] In the above-mentioned case of Perroncito, the average daily growth of the worm amounted to 77 mm., that is to say, only about three inches.

have a custom of eating half-done beef; and in the English regiments stationed there, *Tænia saginata* is of frequent occurrence, inasmuch as some of the soldiers adopt the same practice. In one case the disease broke out three months after the march, and indeed not in a few, but in from fifteen to twenty cases. After two years' residence, about a third part of the soldiers were infected with the tape-worm. Only the officers, whose food consists principally of mutton, which is also prepared in a cleanlier and more careful way, are, as a rule, exempt. The Hindus are still more free from it, since they live entirely upon vegetables.

In respect of frequency of occurrence, Arabia and Syria are little behind India. This is shown, for example, by the fact already mentioned, that a French naval ship stationed off the Syrian coast, whose crew had procured their supply of beef from the shore, and had devoured much of it in the form of beef-steaks *à la Tartare*, had, after a short time, a considerable number of cases of tape-worm (19 out of 152 men).[1] We also learn from Kaschin that among the Buratis inhabiting Baikal every individual is infected with a tape-worm.[2] It is true that these observations were not made on the spot, but in Irkutsk, where the individuals in question were all men who had been garrisoned for years as Cossacks. But in spite of the great distance from their home, they were nearly all infected with tape-worm,[3] and sometimes with several (up to fifteen), which Kaschin took for *Tænia solium*, but which undoubtedly belonged to *T. saginata*. This is seen not only by the description which Kaschin gives of the worm (20 feet long), but from what he tells us of the habits of their hosts. We learn, for instance, that the Buratis live almost entirely upon flesh, especially on that of oxen, sheep, camels, horses, and more rarely of pigs, and that they are so voracious that two men are able to devour at one sitting a sheep two years old. Moreover, this flesh is neither perfectly cleaned nor even cooked, and is eaten from a table which has been used immediately before in cutting up the slaughtered animal, and which has as little acquaintance with water as the vessels and their owners. Fat, liver, and kidneys are eaten raw, and sick animals are as little despised as half-rotten carcases.

Schmidtmüller observed *Tænia saginata* (*Bothriocephalus tropicus*) in Java, principally, it is true, but not exclusively, in the black soldiers imported thither from the coasts of Guinea; and Professor

[1] *Mém. Acad. méd. Paris*, p. 998, 1877.
[2] *St. Petersburg Medical Gazette*, vol. i., p. 366, 1861 (Russian).
[3] In 113 *post mortem* examinations the worms were only twice absent, and their presence was also proved in 500 other persons who were treated in the hospital.

Bälz writes to me from Tokio, that it often occurs in Japan, and is much more frequent than *T. solium.* The case seems to be the same in China, at least many of the French soldiers returned from the Palikao expedition infected with this worm. Fedschenko also found the worm to be widely spread in Central Asia.

Regarding Australia and America, the communications are more scanty, but it is known with certainty that this species is not wanting there. It was also identified by Küchenmeister and myself from Brazil, and by Weinland, Leidy, and Verrill in North America. Weinland, among others, observed it in a Chippeway Indian, but in a form which was very markedly distinguished from the typical *Tænia saginata* by the small size of its proglottides, and by its slender form, so that he was almost tempted to regard it as a separate species.[1] He constituted it a variety *abietina*, and relying upon the branching of the uterus, classed it along with *T. solium*,—erroneously, however, as may be seen from the drawing of the preparation he kindly sent me (Fig. 272).

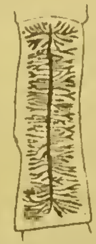


FIG. 272.—Ripe segment of *Tænia saginata* var. *abietina*; after Weinland. (× 2.)

In Europe hardly a country can be mentioned in which *Tænia saginata* has not been found. In fact it is the predominant species of tape-worm in the south and south-west, in Bavaria, Austria, Hungary, Italy, and Turkey. In the north of Germany and in Denmark it has also, during the last twenty years, gradually forced the formerly more frequent *T. solium* into the back-ground. While the cases of *T. saginata* had to be counted by units at the time of the appearance of the first edition of this work, it is now, on the contrary, *T. solium* that has to be sought for. It has become rare, since its relations to the bladder-worm of the pig have become known to an ever-extending circle, and since the fear of *Trichina* has taught us to pay greater attention to the condition of meat.

We possess, however, but few statistics of a definite nature. In Copenhagen, where, until 1869, the relation of *Tænia solium* to *T. saginata* was as 53 to 37, Krabbe afterwards found only 16 examples of *T. solium* among 62 large-jointed tape-worms. According to Grassi, 16 examples of *T. saginata* were found among 19 large-jointed *Tæniæ* in Milan, and according to Marchi, 34 out of 35 in Florence. Similarly all the tape-worms investigated by Bremser in Vienna were, with one exception, hookless, and as this one came

[1] I have, however, no intention of denying that besides the species of the "common human tape-worm," with which we are acquainted, there may be here and there some new ones which are still unknown to us. But there are certainly fewer with us than with the nomadic, hunting and pastoral peoples beyond the bounds of Europe.

from a military hospital, its origin was extremely doubtful. Bremser was at first even inclined to doubt the existence of any hooks in *T. solium,* for which the Vienna tape-worms were taken, until Rudolphi sent him from Berlin the drawing of an armed human tape-worm.[1]

Still more insufficient are the data which have any bearing on the frequency of *Tænia saginata* in Germany and the neighbouring states, since in them the two large-jointed species are almost always associated together. But it may at least be gathered from them that the occurrence of the tape-worm varies in different districts, but that it nowhere attains the frequency with which we have seen it to occur in certain parts of Africa and Asia.

According to the generalisations of the French army surgeons, the tape-worm is twenty-three times as frequent among the soldiers in Algiers as in France. On the ground of these statements, Davaine reckons that in France hardly one tape-worm occurs among 8200 inhabitants, but adds that this number would be too small for Paris.[2] This proportion is also too small for England, as is shown, for instance, by the fact that Bateman, a physician in extensive practice in London, found among every 543 patients one infected with tape-worm. On the basis of results obtained in the Dresden and Erlangen hospitals, Müller reckons, among 3814 *post mortem* examinations, twenty-four cases of tape-worm (nineteen *Tænia solium,* five *T. saginata*); that is to say, 1·168, or about 0·63 per cent., and these were so divided that about 0·13 per cent. were cases of *T. saginata,* and about 0·50 per cent. of *T. solium.* It is, however, a moot-point whether this percentage ought to be regarded, without further investigation, as a standard for the whole population. In Thuringia, according to da Conta, there is one tape-worm patient in every 3315 inhabitants, and in the medical districts of Eisenach, Apolda, Jena, and Weimar, where swine are abundantly reared, and *Tænia solium* is presumably the more frequent, there is one in every 486. In the town of Hanover the tape-worm patients have been reckoned even at 2 per cent.[3]

The variations in the percentages representing the occurrence of tape-worms (and therefore also of *Tænia saginata*) are of course determined by certain local circumstances which are dependent upon the conditions of infection already discussed. These circumstances also enable us to understand how certain classes and occupations suffer

[1] *Loc. cit.*, p. 101. Küchenmeister indeed holds another opinion, for according to him Rudolphi found hooks in a worm sent to him by Bremser as hookless. In consequence of this incorrect version, an unmerited slight is cast on Bremser's credibility.

[2] *Loc. cit.*, t. ii., p. 83.

[3] Compare p. 151, note.

much more frequently from tape-worms than others. It has for example long been known that the female sex is much more frequently infected than the male; and further, that cooks, butchers, and tavern-keepers, in short all those people who have to do with the preparation of animal food, furnish an important contingent of tape-worm patients. This is very well shown by the calculations made by Wawruch.[1] Among 173 tape-worm patients, who (since the observations were made in Vienna) must have suffered mostly from *Tænia saginata*, he found no fewer than thirty-nine cooks, twenty-six maid-servants, and thirteen innkeepers, butlers, and butchers. This does not take into account the large number of housewives, who, as Wawruch's patients belonged chiefly to the lower and middle classes, must have been very generally busied in the kitchen. The proportion of the female tape-worm hosts to the male was almost 2 : 1 (117 : 56). Most of the patients were in middle life (between twenty-five and fifty), when there is, as a rule, a great relish for flesh.

The fact that in the present conditions of European life any opportunity for the acquisition of the tape-worm is, on the whole, somewhat rare, is due mainly to the circumstance that *Tænia saginata* occurs as a rule singly, unlike *T. solium*, whose larval forms, as we have seen, are much more frequently associated than those of the related species. To this fact the former owes its designation "Ver solitaire," which is found so far back as Andry, and was all the more used by the French physicians, since, in consequence of an etymology which we have seen to be erroneous (p. 411), the epithet "*solium*" was also applied to the solitary worm. On the other hand, the very general use of the name in France shows that the tape-worm indigenous to that country is principally *T. saginata*.[2]

But sometimes two or three, or even more, examples of *Tænia saginata* are found in the same intestine,[3] as has been often observed, and is shown, for example, by the fact that Wawruch's 173 patients harboured altogether 206 worms. Of course such great numbers as are found in the Buratis (fifteen specimens in one intestine) can hardly ever occur with us.

From our present knowledge of the life-history and mode of transmission of these parasites, it need not surprise us that, in some cases, several members of the same family suffer at the same

[1] "Praktische Monographie der Bandwurmkrankheit:" Vienna, 1874.

[2] Indeed I have in two cases identified tape-worms procured in France (Paris and Nice) with the above.

[3] From Küchenmeister's work (p. 192) I extract the fact that the Tübingen Pathological Institute possesses four examples of *T. saginata* from one intestine, and that Dr. Pfaff in Zittau also expelled seven from one patient at one time.

time from *Tænia*, or that the disease sometimes assumes an epidemic character.[1]

If it be asked in what way the transmission of the worms takes place, the general answer is, that it is effected by the eating of raw or under-done beef. At least this is the rule, for we hardly need to consider the cases in which infection may have been caused by the goat, or the giraffe, or even by the sheep (for in spite of the above-mentioned negative results, the latter is, perhaps, like the goat, capable of rearing bladder-worms).

The important share that the eating of raw flesh has in determining the occurrence of the worm, has already been shown by the large number of cooks and maid-servants infected with tape-worm, regarding whom it may be added that if they would eat the flesh in the same manner as their superiors, without tasting it beforehand, they would probably hardly have to suffer in any greater proportion. We must also notice the fact which, since Weisse's day, has been often observed, that this parasite is very frequent in persons, young or old, who from dietetic reasons have been fed on raw beef.[2]

It is not, however, only in raw flesh that the bladder-worm is transmitted to the future host, but also in meat in a half-cooked condition, which appears not unfrequently upon our tables in the form of roast beef and beef-steak *à l'Anglaise*. I know definitely, for instance, of one case, in which the *Tænia saginata* originated from a beef-steak, which the host, a colleague now dead, had eaten in Nice. Besides the dishes just mentioned, all those should be deemed suspicious in which the flesh and blood are almost or altogether of their original condition and colour. Only well-cooked, thoroughly boiled or roasted, flesh sufficiently insures us against infection.

Regarding the effect produced on the bladder-worm by the methodical application of a higher temperature, we have, thanks especially to the investigations of Perroncito, a series of interesting conclusions.[3] We learn for example that the motions of the worm, which at a low temperature (up to about 30° C.) were very slight or altogether absent, became extremely lively at 36-38°, but afterwards subsided, and at 44° almost entirely ceased. At 45° C. death ensued, as was shown

[1] For cases of this kind see Davaine, *loc. cit.*, second edition, p. 100. I may also refer to the observation of Knox already mentioned (p. 459).

[2] This is the case not merely in Germany, but also in France and Italy; see for example Levi, "Della frequenza della tænia per l'uso medico della carne di manzo cruda," *Giornale Veneto di sci. med.*, vol. i., p. 169, 1876.

[3] "Della grandine o panicatura," Torino, 1877, and especially "Esperimenti sulla produzione della Tænia mediocanellata," &c., Torino, 1877.

not merely by the turbid appearance of the bladder-worms, but perhaps still more convincingly by the fact that when swallowed (in three cases) they were found to have no effect.

The bladder-worms survived the death of their host only fourteen days (in March); for after the expiration of this time (and sooner in the parts more exposed to putrefaction, such as the tongue), the parasites were all found to be dead. If abundantly sprinkled with water, or dipped in it, they perished in twenty-four hours. A solution of common salt had the same effect, so that the supposition that salt meat might sometimes cause infection with *Tænia saginata* seems somewhat doubtful. Further, the usual way of preparing beef in Italy has at least the effect of completely killing the bladder-worms. A case is mentioned by Perroncito of forty-six persons (ten families, including children and adults, men and women) who twice ate bladder-worms in flesh prepared in the national way, and yet without any individual becoming infected with tape-worm.

On the other hand, a student of Perroncito's who had swallowed a newly extracted living *Cysticercus*, saw the first proglottides leave him fifty-four days later. Fourteen days afterwards he voided, in consequence of an anthelminthic which he had taken, a *Tænia saginata* of 427·4 cm., the number of whose joints was estimated (from below the neck) at 866.

The experiment just mentioned is, however, neither the first nor the only one, directly proving the development of the bladder-worm into *Tænia saginata*. Oliver, an Indian army surgeon, had previously subjected a Mohammedan and a Hindu boy to the same experiment, and, twelve weeks after the swallowing of the bladder-worm, obtained from both the proglottides of *Tænia saginata*.

It is thus clearly shown by the foregoing observations,—the only ones that state with any definiteness the term of the infection—that from nine to twelve weeks must elapse before the *Tænia saginata* gives off the first proglottides. The regeneration will, of course, take a longer or shorter time, in proportion to the size of the remaining neck. If the head be left behind, we generally expect that proglottides will be again voided, in two to two and a half months after the first expulsion. Cobbold reports a case in which medicine was administered three times in succession, whose first application had the effect of expelling a stretch of joints 14 feet in length. On being repeated ten weeks later, 16 feet were voided, and a third dose, nine weeks after the second exit of proglottides, evacuated a stretch of 17 feet. Schimper estimates the average number of proglottides voided in one day at eight to twelve, but this varies greatly, and is often not so large (p. 477). The exit of a larger number (Küchen-

meister speaks of from fifteen to twenty) ought always to be taken as an indication of the presence of several worms.

Attempts to rear the adult worm in animals have hitherto failed. So far as I know, however, these experiments are confined to the case of a dog. During three days, this animal ate hundreds of bladder-worms, but four hours after the last meal, nothing was found but some heads in the stomach and beginning of the small intestine.

The life of the present species seems often to be very long. At any rate it is not at all rare for the patients to evacuate proglottides almost daily for years. One of my Russian students harboured two tape-worms for more than five years. In another ease the disease continued for more than eight years.[1] Wawrueh mentions several cases which lasted from twenty to twenty-five years, and in one case speaks even of thirty-five years. Of course it is doubtful whether this is always the effect of the same tape-worm. If, in a disease that is apparently of long standing, the evacuation of the proglottides cease for months and even for years, and then suddenly begin again, we may safely conclude that the infection has been repeated. Several cases of this kind are recorded by Davaine.[2]

Regarding the death of the tape-worm we know of course even less. But it is very probable that after its death, which of course always severs the former adhesion, it is generally expelled pretty quickly along with the other contents of the intestine, and without undergoing much alteration in form or condition. If it remain longer in the intestine, it may, like the retained proglottis mentioned by Schimper, gradually undergo maceration, and then be ejected in a hardly recognisable mass. In rare cases a kind of mummifieation takes place. The problematieal body which Professor Aitken found in the intestine of a soldier, and gave to Cobbold, who mentions it in his work on Helminths,[3] was nothing else than a mummified *Tænia saginata*, which I could clearly identify from some pieces which were sent me for closer investigation. In addition to this case, Küchenmeister has recently recorded a mummified[4] *Tænia*, observed by Zürn and Meyer, whieh was voided by a strong man suffering from a violent attack of colie. Owing to the kindness of my honoured colleague, I have been able to examine the latter more closely, and have also made the accompanying sketch of it. Like Cobbold's preparation, it appeared to be a nearly cylin-

[1] Cobbold knows many cases in which the patient had suffered from tape-worm for five, six, ten, or even eleven years, and had voided proglottides uninterruptedly. See "Worms: a Series of Lectures on Practical Helminthology," Lect. 4 to 8: London, 1872.

[2] *Loc. cit.*, second edition, p. 102.

[3] "Entozoa," p. 415: London, 1864.

[4] "Parasiten," second edition, p. 96.

drical body, almost like a long and thick thread of pretty firm texture, and with wrinkles and cracks, some of which ran transversely, but most of them in a longitudinal direction. These were partly destroyed by soaking, and then one saw a distinct segmentation, whose traces, when once discovered, were easily observable. The existence of eggs containing embryos in the interior has been already noted by earlier observers. They have lost their spherical form, and by the constriction of one segment have assumed an almost hour-glass shape, as may be not unfrequently observed,[1] if, by the application of strong spirit or otherwise, the water is suddenly withdrawn from them. The small length of the joints and the slender form of the mummified worm, which are much more striking than in Cobbold's case, lead me, however, to suppose that in Zürn's case the parasite was not *Tænia saginata,* but *T. solium.*

Fig. 273.—Piece of a mummified tape-worm (nat. size).

The normal abode of the tape-worm is the small intestine, to the walls of which it is fixed, usually towards the upper end. As may be assumed from analogy to related forms, the head is usually sunk in the villi of the intestine, and covered by them. When in possession of its full vital powers, the worm hangs so firmly that it is necessary to pull and bend it before it will quit its hold. And even after it has done so, it will attach itself again in a moment, if the head succeed in catching hold of a portion of the intestine. Those who only know the worm in its expelled condition can with difficulty form any proper idea of the vital energy and mobility which it exhibits in its normal condition, in the warm intestine of its host. The serpent-like motion and powerful peristalsis of the jointed body, the continuous manifold play of the suckers, and the bendings of the neck, are all phenomena of which those who have seen the worm only in a cold and motionless condition can have no idea.

The tape-worm hangs from its point of attachment in the direction of the stream of chyle, and generally close by the wall, so that its whole length extends backwards within the alimentary canal. As a rule it is straight, but more rarely it exhibits serpentine windings or coils, according to the varying state of contraction of the different parts. Pruner found in one corpse five *Tæniæ* of considerable size,[2] which extended throughout the whole length of the small intestine; and Robin saw one tape-worm which hung through the end of the small intestine into the large intestine, although its point of insertion lay high up near the pylorus, and although its anterior end was rolled

[1] Leuckart, "Blasenbandwürmer," p. 95.
[2] "Krankheiten des Orients," p. 245.

into a coil as large as an apple.[1] Sometimes it even happens that the end of the tape-worm protrudes from the anus during defæcation, and on any attempt to remove it (as Andry has observed), quickly withdraws again into the intestine (p. 425, note). The knots which are sometimes observed on the thin anterior body of expelled worms, can hardly be regarded as normal structures, since they probably arise only from the unusual cramp-like contractions, caused by the use of anthelminthic medicines.

If the stream of chyle turn in consequence of powerful antiperistalsis (especially in vomiting), the position of the tape-worm in the alimentary canal may be occasionally reversed—that is to say, the posterior end may be turned forwards. Cases are known in which the whole or portions of the tape-worm have been vomited,[2] and in one case forty yards are said to have been ejected in this way (van Doeveren). Lavalette, a French physician, has lately reported the case of a pregnant woman who expelled the proglottides singly through the mouth.[3]

Where abnormal openings occur in the alimentary canal, like the so-called fæcal or intestinal fistulæ, the proglottides, and even whole worms, occasionally find an exit through them (Richter, Spoering). We are even informed of an instance in which the tape-worms broke through the wall of the abdomen through a newly formed abscess,[4] so that it almost appeared as though the worm had caused the formation of the abscess, although the nature of the tape-worm body hardly permits us to suppose that it could bore through the intestine, if the latter had not been already in a diseased condition.[5] Especially interesting, in this connection, is a case mentioned by Herz, in which the tape-worm (whether it was *Tænia saginata* is, of course, uncertain) issued through the navel, without, however, bringing any of the contents of the intestine along with it, so that the patient could be dismissed as cured a few days after the exit of the worm.[6]

Of a similar nature are the rare cases in which the tape-worm was expelled through the urethra. In such cases, even when the ordinary signs of vesico-rectal fistula are wanting, it is evident that the worm can only have reached the urinary apparatus from the intestine. In one of the three cases mentioned by Davaine, the tape-worm remained

[1] *Journ. de med.*, t. xxv., p. 222, 1766.

[2] See the cases collected by Davaine, *loc. cit.*, p. 100.

[3] Quoted by Davaine, *loc. cit.*

[4] *Ibid.*, p. 114.

[5] Like Göze and other observers, I have repeatedly found *Tænia pectinata* living free in the body-cavity of the rabbit, but have never succeeded in finding any wound in the intestine.

[6] *Med. Zeitung des Vereins für Heilkunde in Preussen*, p. 75, 1843.

a year in the bladder, and expelled single proglottides at intervals of about eight days, until it was killed by an injected anthelminthic and then expelled at once.[1] We need hardly add that the expulsion of proglottides through the urethra is accompanied by violent and painful disorders, and that the above-mentioned worm-abscesses interfere in many ways with the health of the host.

Besides these, the presence of a tape-worm in the intestine gives rise, under some circumstances, to protracted disease. I say "under some circumstances," for in many cases the health remains unimpaired in spite of the uninvited guest. This happens especially in the case of young children and healthy persons, while, on the other hand, and particularly where there are previous nutritive disturbances and nervous irritability, many and various diseases may be caused by the parasite. As a rule, however, there is an exaggerated fear of the pain excited by the tape-worm. There are some whose complaints begin the moment that they discover the presence of the parasite, although they have perhaps harboured it for months; and others who, after having undergone a tape-worm cure, continue to feel their former pains, although, perhaps, they have long been rid of the worm. Just as physicians speak of a "*hypochondriasis syphiliticorum*," there often seems even more occasion to diagnose a "*hypochondriasis tænio-sorum*."[2] We have already noted that, in contrast to the disfavour with which we regard the worm, the Abyssinians consider themselves ill when they are without it, and regard it as having an advantageous influence on their health. Only if it become too long do they think that it causes any disorder.

In Europe, too, it is sometimes asserted that the tape-worm has a medicinal value. This idea is, however, erroneous; for in cases in which *Tæniæ* of the dog (especially *T. marginata*) occurred in the alimentary canal of the host, I have not unfrequently observed a diseased condition of the intestinal mucous membrane (injection, desquamation of the epithelial layer, and even little ulcers), and, as I have already observed, there could be no doubt that these were due to the parasite.

The disorders usually caused by the tape-worm are partly local and partly of a general nature. And among the former, besides the troublesome and disagreeable tickling occasioned by the spontaneous emigration of the proglottides, we find frequently recurrent disturbances of digestion and colic-like pains, which are felt sometimes at one place and sometimes at another, especially during fasting, being quieted for a time by food and drink. Sometimes the patients have

[1] Darbon, *Archiv. de Med.*, t. v., p. 351, 1824.
[2] For such cases see Cobbold, "Worms, &c.," p. 14.

also a feeling as though the worms were heaving up and down inside the intestine. And indeed it is quite conceivable that the powerful contractions of *Tænia saginata* have an influence on the condition of the intestine. The projecting borders of the joints thus rub in a file-like manner over the villi, and easily produce a congested state, which lasts a longer or shorter time according to circumstances, and gives rise to many diseased symptoms. Moreover, diarrhœtic stools rarely continue in tape-worm patients, and there is often, on the contrary, an irregular alternation of diarrhœa and constipation.

If the disease continue long the nutrition suffers. From this there often arises a condition which has a certain resemblance to anæmia, and which especially exhibits the many neurotic symptoms of this disease. Singing in the ears, hallucinations, giddiness, fainting, pains in the joints, epilepsy, chorea, and even mental diseases, have all been observed to be caused by the tape-worm, and not unfrequently to disappear on the removal of the latter.[1]

It is easy to see, however, that these cases, although so numerous, contain little that is characteristic. They might arise from other causes as well as from the tape-worm. A certain diagnosis is therefore impossible. To this end one must observe eggs or proglottides of the *corpus delicti*, and these must always be identified, before so radical a cure as treatment with anthelminthics is begun.

b. *Cystic Tape-Worms with Circlet of Hooks.*

(Cystotænia, sensu stricto.)

Tænia solium, Rudolphi.

Göze, "Eingeweidewürmer," p. 269 (*T. cucurbitina plana, pellucida*).
Küchenmeister, "Ueber Cestoden," p. 85.
Weinland, "Essay on the Tape-worms of Man," p. 32.

In size, thickness, and number of segments, this species is considerably less than the last. In its extended condition, the length rarely amounts to more than from 3 *to* 3·5 *metres, and in preserved specimens it is generally less than* 2 *metres. The greatest breadth, which is attained about the middle of the body, hardly ever exceeds* 8 *mm. The number of the segments may be estimated at about* 850, *and of these not more than* 80-100 *are ripe proglottides. These make up a third of the whole length, and at the end of the chain attain a length of* 10-12 *mm., and a breadth of* 5 *mm. The head is about the size of a pin-head, and has a spherical shape with somewhat prominent suckers. The apex is not unfrequently*

[1] For further information regarding the diseases of tape-worm hosts, and an account of a number of interesting cases, see Davaine, *loc. cit.*, p. 101.

coloured by a black pigment, and bears a medium-sized rostellum, with generally twenty-six or twenty-eight hooks, which are distinguished from those of the allied species by their compressed and rather stout form, and by the relative shortness of their roots. Following the head there is a thread-like neck, a centimetre in length, whose segmentation cannot be easily detected by the naked eye. The first segments are extremely short, but those succeeding gradually increase in length, so gradually, however, that they only assume the rectangular form at a distance of 1 *metre, or even more behind the head. More posteriorly, the ripe segments begin, the sexual organs having been fully developed about* 200 *joints anteriorly, or at about the* 450*th joint. The ripe proglottides are only rarely spontaneously voided, and generally find an exit, singly or in numbers, along with the excreta. The sexual opening is situated behind the middle of the joint. The uterus, which is generally seen distinctly through the envelopes of the body, has seven to ten lateral branches, which are separated from each other by considerable distances, and in their turn again divide into a number of dendritic or comb-like branches. The eggs are almost round and are enclosed in a firm shell, whose outside is covered with thickly set little rods. Sometimes the original clear egg-membrane persists within the shell.*

FIG. 274.—Head of *Tænia solium.* (× 45.)

FIG. 275.—Half-ripe and ripe joint of *T. solium* (nat. size).

FIG. 276.—Two proglottides of *T. solium* with uterus. (× 2.)

The corresponding bladder-worm (Cysticercus cellulosæ) *has a special preference for the muscles of the pig, but is occasionally found in other*

places and in other animals, as in man. Its occurrence, in the pig at least, is usually very abundant. The caudal bladder is of moderate size (8-10 mm.), and in the muscles has an elliptical form, the longest diameter being in the direction of the course of the fibres. It contains a spirally rolled and much wrinkled head-process.

The species which we have just attempted to characterise, and have designated by Linné's name *Tænia solium*, is by no means identical, as we have already seen, with the similarly named species of the former helminthologists. "The common human tape-worm," to which they gave this name, is a collective species, which includes both Rudolphi's hook-bearing *Tænia solium* and the hookless *T. saginata*. Although both species are even yet frequently included in one, especially in foreign countries, we do not require to prove, after the foregoing discussion of the history and peculiarities of *T. saginata*, that it is justifiable and even necessary to regard them as two markedly distinct species. The size, armature, uterine structure, and development exhibit such characteristic features in either species that a union of the two is impossible. It is especially the mode of development which decides the matter, for it shows that the differences of structure which were formerly supposed to be due only to some subsequent variation, are present from the first.

Origin and Development of the Bladder-Worm of the Pig, (Cysticercus cellulosæ, Auett.).

To Küchenmeister is due the permanent merit of having first discovered the relations between the hook-bearing *Tænia solium* and the common bladder-worm of the pig—the *Cysticercus cellulosæ* of earlier helminthologists—and of having thereby given a proper direction to our views regarding the life-history of this parasite. What induced Küchenmeister to claim the bladder-worm of the pig as the larval state of the tape-worm, was principally the structure of the head and hooks, which so perfectly correspond in the two forms, that the most careful investigation can establish no differences between them.[1] The differences in pigmentation which are occasionally observed, and which consist mainly in the head of the bladder-worm being of a lighter shade, or indeed entirely without colour, can form no obstacle to an association of the forms, especially as it is well known that the adult tape-worms exhibit many variations in this respect.

Küchenmeister's statements had of course the effect of defining in a more satisfactory manner the question regarding the origin of *Tænia*

[1] "Ueber Cestoden im Allgemeinen," pp. 78, 89, 1853.

solium, and confirmatory opinions were immediately expressed.[1] But his view did not obtain general acceptation until the connection of the two parasites was firmly established on experimental grounds, and that principally by the proof that *the eggs of* Tænia solium *develop in the pig into the familiar bladder-worm of the muscles, and also that this is the larval form of the* Tænia.

The first attempt of this kind was made by van Beneden, who fed a pig with a tape-worm, and four and a half months afterwards found it to contain bladder-worms.[2] No proof was given, however, that these bladder-worms originated from the eggs of the worm administered, so that the result of the experiment cannot be regarded as completely convincing. But any doubt which might have existed on this point has been entirely removed by the experiments of Haubner and Küchenmeister.

Haubner administered[3] at different times single proglottides and larger pieces of tape-worm to five young pigs, which came of a brood free from bladder-worms, and succeeded thereby in infecting three of them with bladder-worms. The two other pigs remained uninfected in spite of the feeding; but this negative result cannot in any way affect the cogency of the argument, since in the three other cases the degree of development of the bladder-worms was proportionate to the period that had elapsed since the feeding.

The first pig was killed thirty-two days after the first feeding and thirteen days after the last. It harboured in different parts of the body isolated bladder-worms, altogether about forty or fifty, the majority being found in the neck. The largest were about the size of a hemp-seed, and showed the first rudiment of the head as a minute opaque spot.

The second pig was dissected forty-six days after the first and twenty-seven days after the last feeding, and was found to contain several thousand bladder-worms, which were distributed over the whole body,—some of them being as large as a pea, while the smallest were about the size of a hemp-seed. Microscopic investigation revealed in the more advanced bladder-worms a distinctly formed head, with the rudiments of hooks and suckers at various stages of development. The head-process shone through the walls of the

[1] I was the first to express myself frankly, and indeed on the ground of my own investigations, in favour of Küchenmeister's statements. I frequently had heads of different bladder-worms submitted to me by scientific friends for examination and identification, but could never succeed in distinguishing those of *Cysticercus cellulosæ* and of *Tænia solium* from each other, and always regarded them both as heads of the same species, like those of *Cysticercus tenuicollis* and *T. marginata*, &c.

[2] *Ann. sci. nat.*, t. i., p. 104, 1854.

[3] *Gurlt's Magazin für Thierarzneikunde*, p. 105, 1855.

bladder in the form of an opaque spot. In the third pig, killed sixty days after the first and forty-one days after the last feeding, such a large number of bladder-worms were found, that a single half ounce of flesh contained 150. The largest were almost mature as regards size, form, and the development of the head, while the smallest were like the largest ones in the second pig.

An experiment made by me at almost the same time afforded exactly the same result. There were also five pigs, most of which I fed several times with tape-worm (expelled by various anthelminthics, and especially by cousso and pomegranate bark). I examined the pigs at varying intervals after the commencement of the experiment.[1]

In one case a dissection was made of the animal forty and thirty-two days after the first and last feedings respectively. The bladder-worms were extremely numerous, from 1 mm. to 5 mm. in length, and the largest were already oblong in form. They were found chiefly in the muscles of the belly, breast, and neck, also in the diaphragm, and a few in the brain and liver. The parenchyma of the lungs contained a number of small white cysts, probably representing a brood which had found ingress, but had not become further developed. The head-process was distinctly visible in all of them, but was generally small, and, even in the largest bladder-worms, still without any trace of suckers and hooks. And if it were *à priori* probable that the bladder-worms originated from the administered tape-worm, this was established beyond all doubt by the fact that a muscle extracted from the pig ten days after feeding contained as yet no bladder-worms.

The sterno-hyoid muscle of a second pig, fed in the same way, exhibited, after forty-two days, bladder-worms of the same stage of development as the above case, but surprisingly smaller, although the animal was fed with equal portions and belonged to the same litter. The dissection was not made until 124 days after the feeding, the animal having twenty days previously eaten a second tape-worm. The bladder-worms had meanwhile attained a length of 12 mm., and a breadth of 5·5 mm. They were fully developed, having a head-process 3 mm. long. In number they amounted to some hundreds, while in the first pig there would be, perhaps, as many thousands.

The majority of them were found in the muscles of the breast and neck, and also in the brain; but in the latter situation the parasites, although fully developed, hardly measured more than 5 to 6 mm. The last feeding seemed to have been almost without results. Only in the brain some small bladder-worms were found of 1·5 to 2 mm. in length, and with a newly formed rudimentary head.

[1] Two of these experiments have already been mentioned in my treatise, "Blasenbandwürmer," p. 48, 1856.

The examination of the third pig, which had been fed three times, took place 107 days after the first, seventy-one days after the second, and forty days after the last feeding. Even while cutting through the skin, I was convinced that the experiment had succeeded. The bladder-worms were so abundant, that in many places the flesh seemed changed into a honey-combed mass, somewhat like the spawn of frogs or fish, and the number of the parasites amounted to at least 12,000. The heart, lungs, and brain contained them, although in smaller numbers than the locomotor organs. Instead of bladder-worms, the liver exhibited only some tubercle-like nodules: the eyes were also free from bladder-worms—that is to say, the ball of the eye—for many were contained in the muscles of the orbit, and there were also some under the conjunctiva. The largest bladders had a longitudinal diameter of about 8 mm., while the smallest, which occurred in the brain, measured only 2·5 mm. The other bladder-worms in the brain were also smaller than those in the rest of the body, for the largest did not exceed 4·5 mm. Most of them lay free on the surface of the hemispheres, below the pia mater, or between the convolutions. Others were sometimes free in the ventricles, between the convolutions, and sometimes embedded in the substance of the brain, and then enclosed in a sort of capsule. Some specimens were also found between the lamellæ of the dura mater; these formed projections which had left deep impressions on the internal surface of the roof of the skull. As regards the stage of development of the head, the parasites might be divided into three groups, which probably corresponded with the three feedings. The largest were fully developed, others exhibited various earlier stages of the hooks and suckers, while the youngest had only the first rudiments of a head. The latter were found exclusively in the cavity of the skull, from which, however, the representatives of the second stage seemed to be absent.

The fourth pig, which was killed eighty-two and twenty-nine days after the first and second feedings respectively, appeared at first quite healthy. Only after a long search was a single bladder-worm found deeply buried in the muscles of the neck. It was the size of a large pea, and was fully developed.

In the case of the fifth pig, as in the first and second, excisions of muscles were made from time to time, in order to study the gradual development of the bladder-worms, which were again present in considerable numbers. Eight days after the feeding, no parasites could be found, but many were visible on the second and third excisions, which were postponed till the thirtieth and ninety-fifth days. The pig, which had meanwhile been subjected to other experiments, lived for some time, and on dissection (six months after the feeding) it ex-

hibited perhaps 2000 to 3000 full-grown bladder-worms, which, with few exceptions, were confined to the peripheral muscles of the body.

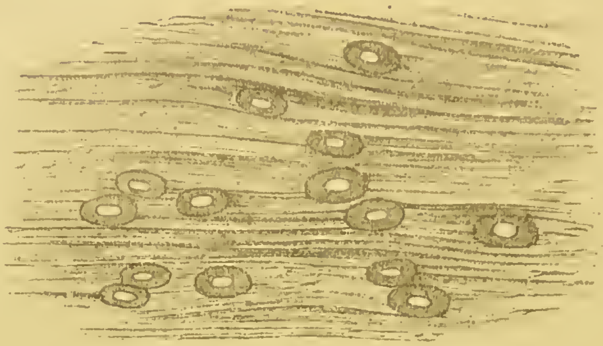


FIG. 277.—Measly pork (nat. size).

The experiments which we have mentioned are not, however, the only ones of the kind. Similar investigations have often been made since, especially by Mosler[1] and Gerlach,[2] some of whose observations we shall shortly notice more particularly. I have also been able to give the results of some new feeding experiments.[3] The results agree in all points with the foregoing statements, so that there can no longer be the slightest doubt regarding the relations existing between the bladder-worm and *Tænia solium*. This might certainly have been affirmed sooner, but any new idea makes but slow progress. Yet even after these experiments had been made, not only by van Beneden but by Haubner and myself, an attempt was made to weaken their cogency by the objection that the investigators had possibly procured the animals for their experiments from districts in which the tape-worm disease was an epidemic.[4] This is assuming, very unwarrantably, that our conclusions are based merely upon the presence of the worms after the feeding. On the contrary, whoever examines these conclusions impartially will be convinced that their cogency is due to a much greater extent to the constant correspondence of the degree of development of the bladder-worms with the duration of the experiment. The mere presence of the parasites might possibly be explained in some other way, although the number of pigs infected with bladder-worm could hardly amount anywhere to eighty or even more per cent.,

1 "Helminthologische Studien und Beobachtungen," p. 43, 1869.

2 *Zweiter Jahresber. d. k. Thierarzneisch. Hannover*, p. 66, 1870.

3 First German edition of this work, Bd. i., p. 745.

4 See Davaine, *loc. cit.*, first edition, p. xxx. In his second edition, indeed (1877), Davaine abandons his hesitation. Even he now acknowledges the cogency of the feeding experiments. But it is very strange that the most convincing one of all—namely, my own—which is the only one that proves the development of the bladder-worms within the same host (as before), is passed over in silence (*loc. cit.*, p. 913).

but the gradual progress of the development in proportion to the duration of the experiment admits of only one interpretation.

Nor is even this consideration necessary to refute this objection. The validity of the experiments is obvious. Shortly after the commencement of one of my experiments, I was directly convinced of the absence of bladder-worms in two of the animals. And some weeks later the muscles were inhabited by thousands of young bladder-worms. In view of these facts, could there possibly be any doubt?

The differences in the number of resulting bladder-worms do not, of course, affect our conclusions; nor do a few negative results. They only prove that the development of the tape-worms, as of other Helminths (p. 85), is determined by certain conditions, which are differently expressed in different animals. Even where the bladder-worms were most numerous, only a few of the introduced eggs had reached maturity. The pig with 12,000 bladder-worms had eaten three tape-worms. If we allow each of these sixty ripe joints, and take the space containing eggs at 6 cub. mm., then the total number of eggs (which have a diameter of 0·06 mm.) cannot have been less than a million, of which only about 12,000, or about 1 in 100, reached maturity. A single tape-worm joint might theoretically produce about the half of those 12,000 bladder-worms!

It must at present remain undecided whether Gerlach's report be correct or not, that only young pigs are capable of infection. He asserts that at an age of six to nine months feeding experiments always fail.[1]

The experimental proof of the specific identity of *Tænia solium* and *Cysticercus cellulosæ* is furnished not only by the rearing of bladder-worms, but also by the metamorphosis of the latter into the tape-worm.[2]

Küchenmeister made an experiment in which, through the prison medical officer, seventy-five pieces of bladder-worm from the pig were given to a condemned criminal during the last three days of his life. They were concealed partly in cooled soup and partly in sausage. Some days before, for want of *Cysticercus cellulosæ*, a *C. tenuicollis* and six pieces of *Cysticercus pisiformis* had been given to the criminal. When the corpse was examined forty-eight hours after death, ten young *Tæniæ*, mostly 3·4 mm. long (with one of 6·8 mm.), were found in the small intestine. By the nature of the posterior part of their body, they showed distinctly that they had just left their cystic state. Unfortunately only four of these young tape-worms were

[1] *Loc. cit.*, p. 67.

[2] *Wiener med. Wochenschr.*, No. I., 1885.

provided with hooks. Although these forms were in Küchenmeister's opinion indubitably derived from *Cysticercus cellulosæ*, yet, considering the different species used in feeding, and the slight development of the *Tæniæ* found, and the striking smallness of the number, some doubt as to the cogency of the argument is not unreasonable.

Thus it seemed very desirable that such experiments should be repeated, and an opportunity soon offered. A young educated man of about thirty years of age, and of healthy constitution, to whom I had explained the development of the tape-worm, offered himself in the interest of science as the subject of experiment. He swallowed in my presence four bladder-worms, which I gave him in luke-warm milk, after cutting off their caudal bladders. Two and a half months afterwards he observed in his stools detached segments of a tape-worm with which he had never before been troubled. The experiment had thus succeeded, and four weeks afterwards I examined two worms about 2 metres long which had been voided by the patient after a few doses of cousso. Only one of these had a head, which of course exhibited the structure of *Tænia solium*.[1]

I made two other experiments, each time with twelve bladder-worms. The one case was that of a man bribed by money, who suffered from Bright's disease; the other that of a consumptive patient suffering from profuse diarrhœa, who served unconsciously as the subject of experiment. Both were without result.

According to the memoirs of van Beneden and Davaine, a student in Geneva, Humbert by name, made a similar successful experiment upon himself. Before the eyes of Vogt and Moulinié, he swallowed fourteen bladder-worms from the pig, and voided the first proglottides during the lapse of the third month. After taking a purgative, the patient remained for a long time apparently free from his worm, but some months later he again noticed the expulsion of proglottides. These exhibited, as before, all the characters of *Tænia solium*.[2]

Similarly Hollenbach, who swallowed a teaspoonful of bladder-worms, expelled five months afterwards a piece of tape-worm five feet long, with many joints, but without the head.[3] It was referred to *Tænia serrata*, but must have been the ordinary human tape-worm, being designated as above only on the authority of v. Siebold, who, as is well known, denied for a while the specific distinctness between the large-jointed *Tænia* of man and of the dog (p. 405).

[1] "Blasenbandwürmer," p. 53, 1856.

[2] So Bertolus reports "Dissert. sur les métamorph. des céstoides," (Thèse de Montpellier, No. 106, December 1856, cited by van Beneden, "Zool. méd.," t. ii.).

[3] *Wochenschrift d. Thierheilkunde u. Viehzucht*, Adam and Niklas, Bd. ii., pp. 301 and 353.

A scrupulous critic may perhaps find these experiments not altogether satisfactory. All the more important is the result of a further experiment made by Küchenmeister on a condemned criminal.[1] Several months before execution the criminal ate twenty bladder-worms of the pig introduced in a sandwich of sausage. They were administered on the 24th November 1859 and on the 18th January 1860, and the execution took place on the 31st March 1860. The result was the discovery of nineteen tape-worms in the intestine. Eleven of these were short (at most five feet) and thin, but already provided with ripe joints, some of which were still adherent, whilst others were creeping about freely in the lowermost part of the intestine. The other eight worms were nearly mature.

Heller has lately reported another such experiment.[2] Eighteen days before death, a consumptive patient ate twenty-five pieces of fresh bladder-worm. On *post mortem* examination, twelve tape-worm heads were found in the intestine, which showed all the characters of *Tænia solium*, but were all very small, and had no joints visible to the naked eye.

Before such facts the last doubts must vanish. We may safely regard it as fully established that *the hook-bearing Tænia solium springs from the Cysticercus cellulosæ.* Only those can continue to doubt who do not wish to see the truth.

The chief host of the *Cysticercus cellulosæ* is the pig. But it is not the only animal besides man which harbours this form. According to Diesing, this muscle-bladder-worm has also been found in apes, dogs, bears, rats, and deer. Though it occurs but rarely in these animals, we cannot leave the fact out of account, especially in considering the mode in which infection may take place, for the specific identity of these forms with *Cysticercus cellulosæ* has been in some of these instances distinctly established. Apart from those found in the apes, which even Treutler[3] identified, those occurring in the roe have been carefully investigated and identified by Krabbe,[4] and by myself. The hooks, which were arranged in fourteen or fifteen pairs, were somewhat thinner and smaller than in the common bladder-worm of the pig, but were otherwise in entire agreement, so that there was no reason to doubt their identity. Even the bladder-worm with twenty-six hooks found by Cobbold[5] in mutton

[1] *Deutsche Klinik*, No. 20, 1860.

[2] Ziemssen's "Handb. d. sp. Path. u. Ther.," Bd. vii., p. 597; English translation, "Cyclop. Pract. Med.," vol. vii., p. 712: London, 1877.

[3] "Observat. path.-anat.," p. 26, Lipsiæ, 1792. I have myself identified a bladder-worm from *Inuus ecaudatus* as *Cysticercus cellulosæ.*

[4] *Vidensk. Meddel. Naturhist. Foren.*, Tab. v., 1862.

[5] "Entozoa," p. 30: London, 1869.

could (from his description) be scarcely distinguished from the ordinary bladder-worm of the pig, although my respected friend is inclined to regard this as an example of a yet unknown species—the hypothetical *Tænia tenella*, Cobbold.[1] Further, an attempt I made to infect the sheep with *T. solium* had only a negative result. Maddox[2] also describes a hooked *Cysticercus* from the muscles of the sheep, but regards it not only as a new species, but as a sexually mature animal (*Cysticercus oviparus*). We must, of course, remember that our knowledge of bladder-worms from the muscles is not yet by any means complete, as is evidenced by the above-mentioned (p. 405, note) *Tænia Krabbei*, which Moniez reared in the intestine of the dog from the bladder-worms of the reindeer. Under such circumstances, we must leave it undecided whether the bladder-worm from the muscles of the alpaca (which seems to be very frequent in Peru, since the four animals investigated by Sappey were infested to an extraordinary extent[3]) should be identified with the *Cysticercus cellulosæ*, especially since we do not yet know whether or not it is provided with hooks.

It is quite otherwise with the bladder-worms of the dog, which, according to Leisering's observations,[4] are distinctly identical with the bladder-worm of the pig, although my attempt to rear them in the dog from the eggs of *Tænia solium* was as unsuccessful as my previous attempt in regard to the sheep. In Leisering's case the bladder-worms were found not only in the muscles but also in the lungs and liver.[5] They were distinguished by their unusual size, but in the viscera they were mostly dead and shrivelled up. J. Vogel gave a similar account a long time before of a blind and apathetic dog whose brain was completely penetrated by *Cysticerci*.[6] In the cat also I once found a single large *Cysticercus cellulosæ* under the right shoulder-blade.

Development and Growth of Tænia solium.

In the above discussion of experimental investigations, we have already had the opportunity of following the developmental history of this tape-worm with some completeness. We know not only the different developmental stages which are passed through, but also how these follow one another. The following summary, based largely on my own observations, will show the extent of our knowledge.

1 Not to be confused with *T. tenella*, Pall., which belongs to the modern genus *Bothriocephalus*.

2 *Monthly Micr. Journ.*, vol. ix., p. 245.

3 *Comptes rendus Soc. biol.*, t. ii., p. 178, 1860.

4 *Bericht über das Veterinärwesen Sachsens*, p. 18, 1864.

5 "Pathologischische Anatomie," p. 434.

6 Similarly Gerlach, *loc. cit.*, p. 69.

1. The Bladder-worm (*Cysticercus cellulosæ*).

As to the fate of the embryos, and the ways by which they pass from the intestine to the muscles or organs they inhabit, we have unfortunately but few definite results, but are left to inductive conclusions, which are rendered somewhat doubtful by the limited range and uncertainty of our experiments (p. 339).

The youngest worms we know were seen eight days after the feeding. I have myself sought in vain for these first larval stages. Over and over again I extracted portions of muscle from the subjects of my experiments eight or ten days after the introduction of the eggs, and once sacrificed a whole pig for this purpose fourteen days after the first feeding and twelve after the second, but without result. This blank has, however, been filled up by Mosler's researches.[1] He describes the young bladder-worms as oval vesicles 0·033 mm. long, and 0·024 mm. broad, only slightly larger, therefore, than the former embryos, but further differentiated in that they enclosed granular contents. The six hooks seemed already lost, if one may so infer from his silence regarding them. There was no proper capsule; the worms lay quite free between the muscular fibres. It was only in the heart that Mosler found these parasites after he had looked through all the muscles of the body in vain. The heart was examined with special care, since the animal had eaten some trichinous flesh in addition to the 180 proglottides, and the *Trichinæ* were looked for specially in the heart.

What Mosler has said here is by no means the only existing observation on the first young stages of the bladder-worm of the pig. A decade before, an English investigator, Rainey, also found them.[2] He describes them, however, not as free vesicles, but as spindle-shaped tubes, lying inside the muscle-bundle, bearing a thick coating of bristles, and enclosing countless small kidney-shaped bodies. According to him the latter are the beginnings of the tubes; they are said to collect inside the muscular bundle, and then subsequently to become surrounded with an envelope. After the tube has remained for a while in its place of formation, it is liberated by the bursting of the muscular bundle. Shortly afterwards it casts its skin; the coating of bristles is thrown off, and the contents become, by coalescence of the corpuscles, a tolerably homogeneous granular mass. At the same time the parasite loses its former slender form. It becomes a roundish vesicle, which develops about it a connective-tissue cyst, under shelter

[1] *Loc. cit.*, p. 52.

[2] "On the Structure and Development of the Cysticercus cellulosæ," *Phil. Trans.*, vol. cxvii., p. 114, 1857.

of which it finally develops by increase of size and formation of the head into the familiar bladder-worm.

The observations on which these statements are based relate only partially to the bladder-worm of the pig. The later stages have been correctly determined, but the first phases do not belong at all to the development of the bladder-worm. They are connected with an entirely different parasitic form, namely, with those organisms which we designate as Miescher's tubes, and rank along with the Psorosperm-saecules.[1] In the first edition of this work[2] I proved their identity with the forms discovered by Miescher and Hessling. Subsequent investigators have confirmed this, so that Rainey's reports do not require further refutation. The mistake will, however, be readily excused by all who know the difficulty of the problem.

Gerlach was no more fortunate than I was in his search for the youngest stages of the bladder-worm. In a young pig which died of intestinal inflammation nine days after feeding, no trace of the infection was to be seen. It was different, however, in the case of a young pig which died, without apparent external cause, twenty-one days after feeding. Here there were in the flesh numerous delicate bladder-worm vesicles, transparent, and therefore difficult to detect. They had no enveloping membrane, were about the size of a pin's head, and exhibited a minute transparent point, the first rudiment of the head.[3]

Even before Gerlach, I found[4] in the muscles of a young pig (which had been fed twenty-one days before with about eighty proglottides) young bladder-worms in the form of thin-walled, free vesicles of at most 0·8 mm. in size. They had a spherical form, but were occasionally somewhat narrowed towards the head-rudiment, and provided with a thick border, from which the former projected like a wart. There was no proper cavity to be seen inside, although the cuticle was already somewhat invaginated at the point of attachment. Vessels could not be detected with certainty.

In addition to these developmental forms, I observed others thirty-two days after the last feeding. They occurred in a young pig which had devoured an immense number of ripe proglottides forty days before dissection.

The smallest bladder-worms found were vesicles 1 mm. long by 0·7 broad. They lay for the most part in the muscles, but there were some also in the liver and brain. A proper capsule was present only in those found in the liver. Those in the muscles indeed were also

[1] See p. 199.

[2] First German edition of this work, p. 238.

[3] *Loc. cit.*, p. 66.

[4] *Loc. cit.*, p. 745.

surrounded by connective tissue; for, strictly speaking, the muscular bladder-worms inhabit the inter-muscular connective tissue, but this connective substance is scarcely more strongly developed than usual, and is so far from forming a true cyst, that the bladder-worms fall out immediately when the bundles are separated. The only peculiarity of the surrounding connective tissue is the presence of a finely granular substance, which lies next the bladder, and, on closer examination, is seen to be composed of membraneless cells, which enclose a clear nucleus (0·007 mm.), and are so indistinctly marked off from one another that the irregular processes of the borders seem to flow into one another.

But the bladders were not all of this small size. The great majority were considerably larger—between 3 and 4 mm.—some had even grown to 6 mm. These differences seem so striking, that I can well believe that the smallest bladder-worms had been retarded in their development, and represented a stage which one would look for about the twenty-fourth day.

With the increase in size, the surrounding connective-tissue mass has also gradually attained a more marked development, so that, especially in the larger bladder-worms, one can justly speak of a special, though still delicate, capsule. The form of the bladder has also changed, inasmuch as the long diameter with which the course of the fibres corresponds is now at right angles to the axis of the head, and is in some so much increased, that it bears to the transverse axis the ratio of 6 to 2·5. It is probably, however, only the pressure of the muscles that alters the original spherical form in this way.[1] Similarly we must refer the constantly lateral position of the head-rudiment to the fact that the lateral surfaces of the bladder stand in closer connection with the blood-vessels surrounding the muscular fibres than do the terminal parts. The former have therefore more advantageous conditions of nutrition.

Fig. 278.—*Cysticercus cellulosæ* with the formation of the head just beginning. (× 10.)

The Organization of these bladder-worms is already quite complete, general size and head-structure excepted. Even the smallest are vesicles enclosing a clear, non-granular fluid, and exhibiting in their walls a distinct and abundant vascular system, with ciliary lappets

[1] I may mention that I once found two muscle bladder-worms in the same cyst, in which the bladder-body was elongated only at the free outer ends, while the other segments exhibited a simple semi-crescentic structure. Even the older helminthologists have noted the occurrence of two bladder-worms in the same capsule.—See the collection of these cases by Stich, *Ann. des Charité-Krankenhauses*, p. 169: Berlin, 1854.

in the fine twigs. The thickness of the wall is still but slight (0·07 mm.): it exhibits below the cuticle two layers, of which the outer has a finely granular tough character, and is resolved into countless small cells (0·007 to 0·01 mm.), while the inner consists of larger drop-like vesicles, which probably have something to do with the secretion of the lymph. The vessels run outside of both these sheaths. They consist of wide and narrow tubes, which partially anastomose with one another in a network, and are so arranged that the finer processes mostly lie towards the exterior. Besides the vessels one finds in the cellular layer numerous strongly refracting molecular granules, and delicate muscular fibres running in various directions.

The head-rudiment was perceptible even in the smallest bladder-worms. But it was at first of comparatively small size, and so delicate that the least pressure sufficed to destroy it. The point of attachment could also be distinguished at that early stage, since it was marked by small calcareous corpuscles round about the former papilla, and also by the radiate grouping of the muscular fibres running from it. Very soon the head-rudiment appears at the middle point of the bladder. Accompanying the radial fibres which run from it, there are others which embrace the place of insertion, and not unfrequently mark the region round about with wavy wrinkles. Similarly the adjacent vessels grow in course of time into considerable stems, which run towards the head into which they pass, or, what comes to the same thing, run from the head into the bladder.

In the smallest bladder-worms the head-rudiment was, as we have said, of but small size. It appeared as a plump rounded appendage of 0·12 mm., which was seated on the wall of the bladder, and hung into the cavity in the direction of the smallest radius, corresponding, that is, to the equatorial axis of the oval vesicle. It is penetrated internally by a wide blind canal, which runs down the axis and opens on the external surface of the bladder, so that the cuticle of the latter is continued through the opening into the head-papilla. The wall proper, like the vascular layer of the bladder-wall, consists of small nucleated cells.

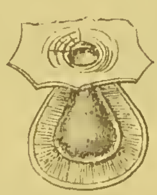


Fig. 279.—Head of *Cysticercus cellulosæ*, with rudiment of the receptacle. (× 25.)

With increase of size the head-papilla soon loses its swollen form. It grows and becomes by elongation a more club-shaped structure, whose internal cavity is enlarged like a bottle at the lower blind end (Fig. 279): when the rudiment is about 0·2 mm. long (in bladder-worms whose longest diameter measures about 1·5 mm.), then histological differentiation begins. Not only can one distinguish on the outer surface a thin

layer of fibres, which pass from the head into the musculature of the bladder, and which must have been previously present in a less developed state, but also cells of another nature lying next the cuticle, which have a different appearance, inasmuch as they assume a spindle form, and impart to the deeper layer a very striking radiate character.

We need hardly expressly mention that the outer muscular layer of the head-rudiment represents that structure which we formerly designated the "receptacle," and which we saw to be of general occurrence in the larger cystic tape-worms (p. 346).

This receptacle lies at first close upon the outer surface of the head-papilla. For a while the two structures grow with perfect uniformity, but soon one sees, in bladder-worms about 2·5 mm. long, that the head-papilla obviously, in consequence of its greater longitudinal growth, curves round in a bow inside the receptacle, and assumes a bent position (Fig. 280). As long as the curve is not very marked, the club-shaped end of the head lies still, almost perpendicularly under the point of attachment, but afterwards it bends more and more to one side, until the angle finally (Fig. 281) comes to lie at the deepest point of the receptacle. The latter thereby loses its former regular shape; the lateral surface which lies next the end of the head is protruded like a hernia; thence it bridges over the angle between the two portions of the bent head, and passes towards the point of insertion.

Fig. 280.—The beginning of the bending of the head of *Cysticercus cellulosæ* inside its receptacle. (× 25.)

Fig. 281.—The head and receptacle of a bladder-worm from a muscle about 6 mm. in size. (× 25.)

In this state the head-rudiment persists until the long diameter of the bladder-worm has increased to about 6 mm.,[1] when it

[1] Since these early stages of *Cysticercus cellulosæ* have not been before observed in man, I may note that similar forms were once (1860) sent to me for examination and identification by my colleague Professor Wagner of Leipsic. They originated from the liver in a case of tuberculosis, were about one line in size, and occurred in considerable numbers, about one for every square inch.

usually measures about 1 mm. But this length is almost equally divided between the two joints, one of which effects the connection with the wall of the bladder to which it is attached perpendicularly, while the other enclosing the enlarged blind end of the head-cavity is bent to the side, almost at a right angle. The receptacle surrounding the head has departed from its previous form in being laterally protruded before the bend of the head. Breadth and height measure somewhat uniformly 0·5 mm. The space running up the axis of the papilla is but slightly enlarged, except at its blind end. It has for the most part the appearance of a narrow canal, and in the basal portion is not straight but of zigzag form, and therefore longer than the linear distance between its ends. This form is obviously the optical expression of a folding of the wall of the papilla, and is sometimes so inconstant that the application of pressure and simultaneous elongation and broadening out of the canal cause it to disappear. The opening of the canal on the bladder appears usually as a transverse slit, whose borders protrude in the form of two narrow lips. The calcareous bodies which surround this slit in a circle have increased in number, and have also spread themselves over the root of the head-papilla. Otherwise, the structure and histology are much as before. Internally, one recognises here and there the subsequent longitudinal vessels, but always only in fragmentary fashion, since they are easily destroyed by pressure.

The early bending of the head-papilla here described is, as far as I know, an exclusive characteristic of *Cysticercus cellulosæ*. In the other bladder-worms known to me the head retains its originally straight position, almost unchanged, until the formation of the suckers and circle of hooks. The flexure, if it occur at all, does not begin till later, when the neck increases greatly in length after the completion of the head. In the bladder-worm of the pig this elongation occurs at an earlier period than usual.[1]

In spite of the marked curvature of the head-papilla, no proper head is yet to be found. The process is indeed enlarged terminally like a club, and the internal canal is markedly enlarged, but there are as yet no traces of suckers or hooks, which are the most important characteristics of the tape-worm head. The next stages, however, result in the formation and development of these organs.

We may pass over the details of the process with a simple reference to our former discussion (p. 351). There we saw how the suckers originated round the enlarged cavity, but the hooks and rostellum

[1] Perhaps the *Cysticercus longicollis* also resembles the bladder-worm of the pig. At least one finds specimens of this worm in which the head-papilla is wound into a spiral, which bears suckers even before the hooks are perfectly developed.

were at the end of the blind process. It sometimes happens, too, that the floor of the cavity (Fig. 281) becomes intruded like a boss, and thus comes to present an appearance which Monicz erroneously regarded as the formation of the tape-worm head (p. 354). It is not this boss which forms the head, but the whole lower end of the head-process—a portion so conspicuous that it includes almost the whole portion which is bent to the side.

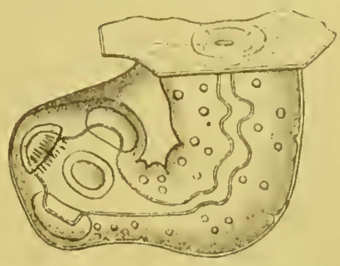


FIG. 282.—Metamorphosis of the head-process into the head proper in *Cysticercus cellulosæ.* (× 20.)

During the development of the later head the process has been continuously increasing in size. The receptacle, too, has gradually grown to a length and breadth of 1·3 mm. or more. The histological development is now complete. One can recognise not only the characteristic musculature of the suckers and of the rostellum, but may also distinguish the muscular fibres running in various directions. In suitable preparations the vascular system is perfectly distinct. It consists of four longitudinal stems, which give off several lateral twigs, and are connected together between the rostellum and suckers by a circular vessel. Similarly the hooks gradually attain complete development. Not unfrequently one sees round about them small isolated points, the remains of the primitive spines (p. 352).

With this process the development of the bladder-worm essentially ends. The changes which afterwards ensue, after the course of the second month, mostly concern only the upper portion of the head-process, which is attached to the still continuously growing bladder-wall. This neck-like portion at first hardly predominates over the enlarged lower portion, but after the formation of the head proper it begins to grow rapidly, and, by the formation of numerous calcareous corpuscles,[1] to present continually a more distinct anatomical contrast to it. In other words, the development of that cylindrical body begins, which is usually intercalated between the head and bladder-wall, and which resembles the subsequent tape-worm body to such an extent that one may for a while consider the two as identical. The growth progresses both

FIG. 283.—Completion of the head-formation in *Cysticercus cellulosæ.* (× 15.)

[1] Moniez is mistaken in disputing the existence of calcareous corpuscles in this worm, "Essai, &c.," *loc. cit.*, p. 57.

in breadth and in length, and that so quickly that the enveloping receptacle rapidly acquires double or triple its former diameter.

In spite of this increase in size, the head-process still retains its early position inside the receptacle. The flexure, however, gradually passes into a spiral curvature, and the head is more or less raised by the growth of the succeeding portion. With increased age and length, the spiral becomes more perfect, so that one finds specimens where the head-process exhibits one and a half turns and more. In its unrolled state the body of the worm measures about 10 mm. long by almost 2 mm. broad. In order to understand how so large a body can find room inside the receptacle, we must remember that the body of the worm is not only spirally coiled, but is also abundantly wrinkled and folded transversely. There are but few bladder-worms where the head-process is equally folded. In longitudinal sections one sees (Fig 286) the boundary on either side raised in long, thin, comb-like processes, interlocking with each other like fingers, and almost filling up the internal cavity. Here and there the folds are also beset with small elevations. Still more striking is the fact that the head-process of the adult bladder-worm seems to stand in no direct connection with the bladder.

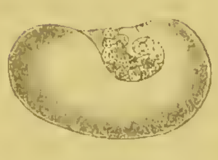


Fig. 284.—The common bladder-worm of the pig, with invaginated head. (× ½.)

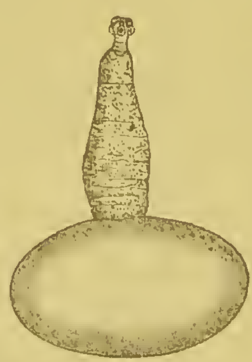


Fig. 285.—The same, with evaginated head. (× 2.)

Fig. 286.—Longitudinal section through the head-process of the same. (× 40.)

Instead of being attached to it, as before, at the margin of the invagination, the latter is now separated off, so that its basal end protrudes freely into the head-cavity, like the proboscis of a gasteropod. The connection between the head-cavity and the invagination opening is thus effected by a sort of outer cavity, including mainly the basal portion of the head-process. It does not remain exclusively confined

to this, but surrounding the greater part of the rolled-up process, as a narrow space separates the latter in many places, as far as the last segment, from the surrounding receptacle.

I must confess that I did not at first recognise this peculiar character of the head-process, which I know only in the bladder-worm of the pig. I first understood it when I became convinced that the formation of this outer cavity, which isolates the head, results from an annular fold which surrounds the base of the latter, and is distinguished essentially from the other folds of the internal space only in this, that it develops to a greater depth, and grows round the whole mass of the head-process like a bell.[1] Traces of this fold are present in other bladder-worms. Thus, for example, in the *Cysticercus* from the crow, described and figured above (p 343), the basal fold has only to be deepened and expanded like a bell in order to isolate the head-process, just as in the adult bladder-worm of the pig.

It is obvious that the "outer cavity," in spite of its peculiar character, represents an integral part of the head-cavity, for its wall exhibits the same folds as we have seen to exist over the whole length of the latter. The outer wall is indeed destitute of these folds, but that is probably because of its slight thickness, and of the tension to which it and the receptacle in general are subject.

This unusual condition of the head-process deserves special notice, if only because the early observers were largely mistaken as to the position and attitude of the latter within the receptacle. This is particularly the case with Robin's figures, reproduced by the elder van Beneden[2] and by Davaine,[3] which are at least false, in so far as they show the head-process rising from the base of the receptacle ("vésicule intérieure," Dav.; "membrane enveloppante," van Ben.). If one press the tænioid body of the bladder-worm out from the receptacle one may indeed see such appearances as Davaine figures (after Robin); but a closer examination shows how false are conclusions drawn from such cases. This fact alone is conclusive, that the body protruding from the rupture shows the head, not in its evaginated state, as Davaine represents it, but invaginated, as it originally appeared, with cuticle and hooks internally.[4] Much more correct and satisfactory are Steinbuch's representations, which, though

[1] The only one who has described this peculiar structure before is Moniez, but he seems to me to have no correct idea of its true nature (*loc. cit.*, p. 56).

[2] "Zoologie médicale," *loc. cit.*

[3] *Loc. cit.*, p. 39, Figs. 3 to 6.

[4] Küchenmeister has figured the circlet of hooks in a bladder-worm head pressed out in this way, as the "Apex of the head (Vorderkopf) of *Tænia solium*" ("Parasiten," first edition, tab. iii., Fig. 8).

dating from the year 1801,[1] are really the best researches on the structure of *Cysticercus cellulosæ* until modern times. He recognises not only the connection between the head-process and the bladder, but knows also that the former is hollow up to the circlet of hooks, and is invaginated in itself, so that, when pressed, it can be protruded from the opening of the bladder like a snail's tentacle. Nor does the existence of the above-described outer cavity escape him, although he does not quite correctly grasp its relations to the receptacle, which even Werner has recognised and described as a *tunica vaginalis.*[2]

Although the head-process is in reality an integral part of the bladder, and, until its separation, is in connection with the organs and tissues of the latter, yet one must not directly identify the two portions in their anatomy and histology. Both differ in fact widely, much more indeed than do the head and joints of the adult tape-worm, whose genetic relations are very similar. These differences include more than the specific organization of the head-proper, and persist between the bladder and the cylindrical body of the worm.

What strikes us at once is the different thickness and firmness of the body-wall. This is thin and tender on the bladder, but acquires a considerable thickness, and a much firmer character when it is continued to the attached process. The connective-tissue becomes less abundant, the musculature greatly increases, and the fibres form, as we have seen, regular layers and bands. The calcareous corpuscles embedded between the latter serve to increase the firmness of the structure. Not less marked is the thickness of the cuticle, which is fully four, or even six, times as great as that of the bladder, although it turns its surface, not towards the exterior, but towards the interior of the body of the worm. The subjacent subcuticular layer is also of considerable thickness. It exhibits the same structure as the subcuticula of the adult tape-worm—indeed the cylindrical body of the bladder-worm is in all essential features like the latter.

1 "De Tænia hydatigena anomala," Dissert. inaug., Erlangen, 1801. As specially characteristic, I may quote these sentences :—" Tæniæ corpus in se ipsum retractum atque mirifice involutum figuram globosam repræsentat" (p. 17). "Vermis corpus canalis membranaceus, cavus, conice elongatus, et rugis seu plicis circularibus compositus est" (*ibid.*). "Extremitas crassior superficiei internæ vesicæ caudalis imposita atque adnata aperturam vesicæ circumdat" (*ibid.*). "Tæniæ corpus quiescens in se ipsum inverse est retractum" (p. 36). "Eodem modo vermis ex se ipso procedit, quo tentaculum Helicis in se conversum atque retractum invertendo ex se ipso prodit" (p. 21).

2 *Loc. cit.*, p. 22.—" Pars corporis vesicæ adhærenti proxima et in vesicæ antrum recedens globuli membranam exteriorem format—(usque ad latus, ubi) corporis vermis membrana in se ipsam intus est reflexa." See also the explanation of Fig. 8—"Tunica vaginalis quam adesse opinatus est Werner, non est nisi pars ultima corpusculi tæniæ sacciformis, quæ superficiei internæ vesiculæ caudalis adhæret ejusque continuationem inæqualem repræsentat."

The wall of the bladder is quite different, for not only is the cuticular envelope tender and the cells of the subcuticula of a more roundish form, but the musculature in particular is but slightly developed, and is composed of fibres which show by no means such a regular arrangement as in the cephalic appendage. One does indeed find bands of fibres which run from the insertion of the head in a meridional and equatorial direction, but a still greater number, especially deep down, run across one another diagonally. We must further note that the fibres form no closed layer, but leave between them more or less wide meshes, which are filled by the cellular tissue. At the angles of the meshes the fibres are often split, and are united together in a still finer network, which penetrates the whole ground-substance. One even sees muscles in connection with the subcuticula, although it is difficult to get a clear idea of their exact nature. Yet the nature of this connection is an interesting point, since it determines that peculiar tuberculated appearance which even Steinbuch[1] emphasised as a characteristic of the bladder-worm of the pig. Somewhat similar elevations (0·05-0·06 mm. broad by 0·025 mm. high) are indeed to be found in the bladder-worm of *Tænia saginata*, but they are much less high and much less regular. The other bladder-worms show, instead of the tubercles, somewhat regular transverse wrinkles, which are, as one can easily see in longitudinal sections of *Cysticercus pisiformis*, occasioned by a fan-like distribution of the meridional fibres attached to the subcuticula. Perhaps, too, the thickness and rigidity of the cuticle, which is much more marked in the bladder-worm just named and in its allies than in those of the human tape-worms, and especially of *Tænia solium*, exercises some influence on the nature and appearance of the bladder-wall. We have already mentioned that the vessels of the bladder-wall are, like the muscles, united into a meshwork. We need only add that these meshes arrange themselves at the sides of the head-process in two broad bands, which run from the ends of the bladder towards the middle, and finally pass as longitudinal vessels into the head-process, becoming connected laterally somewhat like a rope-ladder.

The calcareous corpuscles are distributed singly over the whole wall of the bladder, and are specially abundant in the neighbourhood of the head-process, although never so closely crowded as in the cylindrical body of the worm.

Before reaching this stage of development, the *Cysticercus cellulosæ* must have lived about three or four months. This does not mean,

[1] *Loc. cit.*, p. 11. "Superficies vesicæ externa eminentiis granulosis minutissimis innumerabilibusque obsita est."

however, that it might not sooner undergo a metamorphosis into a tape-worm. Since it is not the whole cylindrical body of the worm, as we shall afterwards see, but only the head proper, which becomes the tape-worm, a shorter time is sufficient to render the transformation possible. After the lapse of two months and a half the head is provided with hooks and suckers, and we may even conclude that the bladder-worm of the pig attains maturity before the close of the third month. The subsequent changes are limited essentially to an elongation of the cylindrical body. According to all appearances this increase in length is not in any way restricted to a certain age, though in course of time it gradually decreases in rapidity. Even the bladder sometimes increases for a while in size, though usually (and particularly in the muscles) it is but little larger than a small bean.

It is difficult to determine accurately how long the bladder-worm may live and retain its potentiality of development. In the case of bladder-worms from human muscle, Stich[1] believes, though on the strength of but few and uncertain observations, that from three to six years may elapse. After this period the bladder-worms, easily detected through the skin, lose their elastic character, and one after the other gradually become smaller, and finally disappear, on superficial inspection at least. The bladder-worms inhabiting other organs, especially the brain and eyes, may indeed attain a much greater age. There are cases of bladder-worms in the brain which have for twelve to fifteen years excited the most critical symptoms,[2] and by help of the ophthalmoscope a bladder-worm in the vitreous humour has been observed and demonstrated for twenty years.[3]

It is no longer necessary to give any special proof of the identity of the common bladder-worm of the pig with this bladder-worm occurring in man,[4] the most careful scrutiny reveals no difference between them, and their mode of origin is the same. It does not follow, however, that it is always and only the *Cysticercus cellulosæ* which infests man. In fact we shall afterwards find that another bladder-worm occurs in man under like conditions, and represents no mere variety, as is the case with other forms, which both

[1] Stich, *Annalen des Charité-Krankenhauses*, p. 170 : Berlin, 1854. For Lewin's criticism, *loc. cit.*, Bd. ii., p. 645, 1875.

[2] See Lewin, *loc. cit.*, p. 645.

[3] Zülzer, *Klin. Wochenschr.*, No. 4, 1876.

[4] This special proof has been furnished by Redon, who swallowed four human bladder-worms, and three months afterwards voided proglottides of *Tænia solium*. Redon over-estimates, however, the importance of his experiment, when he asserts that the identity of the human bladder-worm with the *Cysticercus cellulosæ* was thus for the first time established. (*Comptes rendus*, t. clxxxv., p. 676, 1877.)

ancient and modern investigators have wished to establish as distinct species.[1]

Soon after the discovery of the human bladder-worm by Werner[2] its identity with the *Cysticercus cellulosæ* was recognised by Fischer, and was established by his successors, among whom I would especially mention Steinbuch. Werner is not, however, to be regarded as the discoverer of the bladder-worm of the pig, for the occurrence of bladder-worms in the muscles of man had been detected long before. But they were then in nowise regarded as animals either in pig or man, but as glandular tumours ("glandia"), although their animal nature, at least in the case of those from the pig, had been recognised since the end of the seventeenth century by Hartmann[3] and Malpighi[4] independently of one another. Hartmann further expresses the probability that the other so-called "glandular tumours" also resulted from intestinal worms.[5]

The fact that the bladder-worms were still considered as tumours and degenerated glands, proves only how difficult it is to displace old-established opinions. The idea was, indeed, an old one, for we find it

[1] Besides Köberlé, to whose opinion we shall return, Brera and Cloquet especially have tried to break up the *Cysticercus cellulosæ* of man into several species. ("Compendio di elmintographia humana," 180, p. 24, and "Dict. des sci. med.," t. xxii., p. 165.)

[2] Werner, "Vermium intest. brevis expositionis continuatio tertia," p. 77 : Lipsiæ, 1788. For the first report ou bladder-worms in man, see *Op. cit.*, contin. sec., Lipsiæ, 1880.

[3] "Miscell. curiosa seu Ephem., Acad. nat. curios.," Dec. ii. Ann. vii. 1688, p. 58. A few years previously (1685) Hartmann also recognised *Cysticercus tenuicollis* as a living parasite, and thus for the first time detected the true nature of "hydatids."

[4] "Opera postuma," p. 84, edit. London, 1698. "In suibus verminosis, qui Lazaroli dicuntur, multiplices stabulantur vermes, uude horum animalium carnes publico edicto prohibentur. Occurrunt autem copiosi intra fibras musculosas natium, obvia namque oblonga vesicula folliculus diaphano humore confertus, in quo natat globosum corpus candidum, quod disrupto folliculo leviter compressum eructat vermem, qui foras exeritur et videtur æmulari cornua exmissilia cochlearum, ejus enim annuli intra se reflexa conduntur et ita globatur animal. In apice attollitur capitulum et globati vermem ad extremum folliculi umbilicale quasi vas perducitur." Malpighi had thus even an iutimate acquaintance with the head-process, more accurate at least than Hartmaun, whose description (*loc. cit.*) runs as follows :—"In corde suis glandia complurima, ultra viginti, in parenchymate utriusque ventriculi intimiori observavi : singulos scrobiculos singulæ tunicæ albæ oppleverant ; tunicis incisis peculiaris tenuis membranæ folliculus eximi poterat, qui præter limpidum humorem fuuiculum candicantem fili albi instar convolutum complectabatur, ipsissimum vermiculum." Though Hartmann's description is less intimate than Malpighi's, the right of priority rests with the former.

[5] "Glandia, aut quocunque nomine his affines veuiant pustulæ, nidos esse vermiculorum mihi fit verosimile" (*loc. cit.*). Küchenmeister asserts ("Parasiten," second edition, p. 56), that in this passage, first rescued from forgetfulness by me, I have "unfortunately" falsely translated "uidos vermiculorum" as "worm nests," while it means nothing more than the place occupied by the worms. I will not discuss which translation is the more correct, but will only note that I have never translated this passage at all (see "Blasenbandwürmer," p. 8). Küchenmeister has often been "unfortunate" when he criticises my assertions as "erroneous."

even in the writings of Hippocrates and in Aristotle, who, in his natural history, ranks the bladder-worms (χάλζαι, grandines) among the diseases of swine.[1] The first knowledge of the bladder-worms of the pig is lost in antiquity; some would, indeed, assert that the Mosaic law against eating the flesh of that animal had not a religious but a sanitary basis.

Fresh and more accurate investigations were necessary before the animal nature of the bladder-worms of the pig could be generally recognised. And these were forthcoming; for shortly before Werner's discovery, mentioned above, Otto Fabricius[2] and Göze[3] has brought forward most convincing proof that the structures in question were true bladder-worms. Since this amounted really only to a confirmation of a previous discovery, both investigations remained unacknowledged, but it was no small merit to have established the nature of the bladder-worms for all future time.

2. The Adult Tape-Worm.

The experimental helminthologist can rarely have the opportunity of examining the metamorphoses of the bladder-worm of the pig within man himself. This is not, however, necessary; for though man is the only host infested with *Tænia solium*, he is not the only creature in whose intestine the bladder-worm may attain to further development. Even in other mammals it is possible to follow the first stages, at least, in the metamorphosis. One cannot always reckon with certainty on a positive result, for the experiment often miscarries—the worms are digested, and only the hardly recognisable remains are left. In other cases, however, one finds on examination—which must not, of course, be too long postponed[4]—the first phases of the metamorphosis of the bladder-worm, which entirely agree with what we have seen (p. 382) in the case of the bladder-worm from the rabbit.

To refer only to one of my experiments, I fed a rabbit with about thirty pieces of adult bladder-worm from the pig. The dissection

1 "Histor. Animal.," lib. viii., cap. 31. Here also Küchenmeister detects something erroneous in my statement.

2 *Nova Acta Soc. Hafn.*, t. ii., p. 287, or *Deutsches gemeinnützigcs Archiv*, Jahrg. ii., Quartal i.: Leipzig, 1788.

3 "Neueste Entdeckung, dass die Finnen im Schweinefleisch keine Drüsenkrankheit, sondern wahre Bandwürmer sind": Halle, 1784. The fact that in Göze's great work, which appeared in 1782, there is no mention of the bladder-worm of the pig, has led Küchenmeister (*loc. cit.*) to the false conclusion—"Göze does not know the *Cysticercus cellulosæ*, though Pallas does." I am not aware that the latter has especially considered the bladder-worm of the pig, but Göze has certainly earned a much greater merit by his account of this worm.

4 Heller's statement that the tape-worms introduced perish after twenty-four hours (*loc. cit.*, p. 597, Eng. transl., p. 718) is somewhat too narrow, as the following case shows.

took place fifty-one hours afterwards, and was thus postponed somewhat longer than usual. I was at first afraid that the experiment was to have only a negative result, but in the terminal portion of the small intestine I found twelve young tape-worms close beside one another. Their relation to, or rather origin from, the bladder-worm introduced, was proved by the nature of their hooks. With one exception (Fig. 287), they were all of the same character—small club-shaped worms, scarcely 1·5 mm. long, which exhibited lively movements till they became cold. On microscopic examination it was seen that these worms (Fig. 288) represented essentially only the former head of the bladder-worm. The body, 10 to 12 mm. long, which formerly adhered to the head, was lost, all except the short, thin neck. The former, therefore, does not become a part of the future tape-worm in *Cysticercus cellulosæ*, any more than in *Cysticercus pisiformis* or *Cysticercus fasciolaris*. Only the neck remains as a stalk or stumpy process, connected with the spherical head, which it nearly equals in length but falls far short of in breadth. A small, half-macerated, ragged appendage to the neck is all that remains of the formerly conspicuous body of the worm.

FIG. 287.—Bladder-worm from the pig, after the digestion of the bladder. (× 20.)

FIG. 288.—Head of *Tænia solium* from the intestine of a rabbit, in different stages of motion. (× 25.)

To the above there was one exception (Fig. 287). This still retained a portion of the former body of the worm. The greater part was lost, and the remainder was rapidly going, but it was still large enough to make this one triple the size of the others.

The result was, as we have said, in entire harmony with the results of our investigations of other cystic tape-worms; one fact was, however, striking—that the development had not progressed further in the two days which had elapsed since the introduction of the bladder-worms. In the tape-worms of the dog the above-described state is found twelve to fifteen hours after feeding. At the end of the second day they show a distinct segmentation on the considerably elongated body.

The difference in this case is probably to be explained by the fact that the animal used does not afford the proper *habitat*, which, indeed, is found only in man.

The youngest tape-worms as yet observed in man are those which Küchenmeister found in the criminal fed by him seventy-two and sixty hours respectively before death. These specimens measured from 3 to 4 mm. in length (with the exception of one only which was twice as large), and showed on the posterior end of the body, where the bladder had been attached, a small notch-like constriction, as is seen in all tape-worms immediately after their separation from the bladder (p. 382). Nothing is said about segmentation, but we can well believe that it was present, at least in the larger specimens.[1]

Had the nature of the end of the body been different, we might have taken the young worms for *Tæniæ*, which, by the loss of their joints, had been reduced to head and neck, and were now commencing the formation of a new chain of joints. The changes undergone by the young tape-worm are exactly like those exhibited by a surviving head. The posterior appendage lengthens, and separates into a series of joints, which become posteriorly more and more marked, as they become separated by the intercalation of new segments ever further from their point of origin. At the same time they are rapidly growing in size and development, so that from an inconspicuous head a very considerable chain soon results.

Although *Tænia solium* is decidedly behind *T. saginata* in its size and in the number of its joints, it is still one of the most conspicuous cystic tape-worms, for it exceeds the other species of this group by at least a metre. This predominance is not determined by the proglottides remaining longer united, but, as in *T. saginata*, by a luxurious vegetative growth and formation of joints, which proceed so quickly, indeed, that the individual development is to a certain extent outstripped. As in the hookless tape-worm of man, the joints attain their final size and development only at a considerable distance from the head.

But the form of the tape-worm and the growth of the joints are perhaps best expressed by measurements. I shall first refer to an animal about 224 cm. (that is, about 9 feet long), which was found

[1] Heller reports, in the case mentioned on page 497, that he found "no joints visible to the naked eye" on the "very small" tape-worms, even eighteen days after the transmission of *Cysticercus cellulosæ*. This does not, however, prove the real absence of segmentation, for we may compare it with his other statement that the segmentation in the adult *Tænia solium* begins 3 cm. behind the head. The first joints are so small that they are hardly ever recognisable by the naked eye. The remark that the worms were all very small, leads one also to conjecture that the conditions of development—the experiment was made on a consumptive patient—were but slightly favourable.

neither in strong contraction nor in great extension, and was therefore in so far normal.

The neck was attached to a head 1 mm. broad, and had at first a diameter of 0·45 mm. It exhibited at the end of the first 25 cm. a breadth of 2·2 mm. The number of joints in this length was of course very great. They amounted to 377, of which 112 belonged to the first 2 cm., since the foremost joints were only 0·01 mm. long. The other joints were thus distributed:—the following 6 cm. had 123 joints (of which the last were 0·7 mm. long by 1·2 mm. broad); the next 9 cm. had 82 (with a maximum length of 1·2 and a maximum breadth of 1·4 mm); the last 8 cm. had 60 (with a maximum length of 1·5 and a maximum breadth of 2·2 mm.).

In the second 25 cm. the breadth increased from 2·2 mm. to 4·5 mm., and the number of joints sank to 129. On the first third there were 50 joints (of which the last were 2 mm. long by 3·3 mm. broad); the middle portion bore 42 (with maximum length of 2·2 and maximum breadth of 4·3 mm.); while the third portion had 37 (the last joint being 2·3 mm. by 4·5 mm.).

The third length of 25 cm. contained on each 8·3 cm. 37, 35, and 30 joints respectively—in all 102, of which the last were 6 mm. broad by 3·1 mm. long. The fourth 25 cm. bore 68 joints, with a terminal length of 4·6 and a breadth of 6·6 mm.

The 5th 25 cm.	bore	49	joints, of which	the last were	6·5	mm. long by	6·3	broad.
6th	,,	37	,,	,,	7·5	,,	6·3	,,
7th	,,	29	,,	,,	9·5	,,	6	,,
8th	,,	25	,,	,,	11·3	,,	5·6	,,
9th	,,	23	,,	,,	12·2	,,	5	,,
Last	,,	22	,,	,,	13	,,	4·5	,,

In all, therefore, the worm had 861 joints, but these were so different in size and development, according to position, that the different parts of the chain looked very different. Thus the anterior half consisted of joints whose breadth was decidedly greater than their length, but always decreasingly so, till about the middle of the body the joints were approximately square. In the second half the length was greater than the breadth, and that increasingly so, since the breadth diminished in a marked manner posteriorly. By the middle of the first metre the ratio of the breadth to the length was as 1 : 0·5, in the middle of the last metre as 1 : 2. The greatest absolute breadth occurred at a short distance behind the middle of the body.

We need hardly note, after what was said of *Tænia saginata* (p. 431), that there is a direct connection between the form of the joint and the developmental stage reached by the sexual organs, and

especially by the uterus.[1] It is evident that the joints with preponderating breadth have either no eggs in the uterus, or but few. It is in the square joints that the eggs, which accumulate in increasing numbers as the uterus lengthens out, pass through their embryonic development. But it is only in the extended proglottides of the last metre that the eggs acquire their brown shells and the uterus its final form. Only these last joints exhibit the characteristic dendritic structure and colour of the uterus, which are directly evident to the observer through the thin and almost transparent body-substance The number of these "ripe" joints is at most about 100.

The study of the structure of the sexual organs is therefore important, especially in the examination of the short proglottides. Even before the end of the first length of 25 cm., which includes, indeed, half of the total number of joints, the sexual organs begin to appear. It takes 25 to 35 cm. before they are fully formed. Then copulation takes place, which is succeeded by the passage of the eggs into the uterus and the beginning of the embryonic development.

In order to obtain more data for the decision of the question whether these measurements and proportions have a specific or individual importance, I have lately examined another well-preserved specimen of *Tænia solium.* The worm was somewhat more strongly contracted than the one first measured, being only 175 cm. long, while possessing about an equal number of joints. Before the middle of the body a breadth of 7·5 mm. was attained.

The segmentation began at a distance of 3 mm. behind the head, which was 1 mm. thick, but it was at first faint and difficult to demonstrate, so that I have only approximately estimated the number of joints in the first centimetre at 65. The second centimetre contained 80, the third 57, the fourth 32, and the fifth 41—altogther 414 in the first 5 cm., almost as many as in the other 170 cm. of the body! The small number of joints in the fourth centimetre was explained by the fact that it had undergone an unusual extension, so that some of its joints measured 0·3 mm.,—much more than in the following portion, in which even those at the end did not exceed 0·2 mm. In the three previous portions the length of the joints rose to 0·08, 0·1, and 0·17, and the breadth to 0·7, 1, and 1·6 mm. respectively. The fourth much extended portion showed the same breadth at its termination, the fifth a breadth of 2·5 mm. Thence the size of the joints increased so rapidly that the next length of 20 cm. exhibited only 229 segments,—

[1] We must also remember that the form of the joints is largely—though here less strikingly than in the very muscular *Tænia saginata*—determined by the state of contraction exhibited by the worm, a fact which prevents any absolute accuracy in these measurements.

a number which in the following lengths of 25 cm. sank to 138, 76, 47, 33, 26, and 22, so that the total number of segments was about 848.

The 229 segments, after the first 414, were so distributed that 98 belonged to the first 5 cm., 61 to the second equal length, and 70 to the remaining 10 cm. At the end of these three portions the length of the joints was 0·3, 0·9, and 1·2 mm., with a breadth of 3, 3·9, and 5 mm. respectively. The other relations may be best seen from the following summary, to which we must add that the first 25 cm. contain not less than 414 segments:—

The 2d 25 cm.	contain	138	joints,	of which the last are	2	mm. long by	6	mm.	broad.
3d	,,	76	,,	,,	3	,,	7·5	,,	
4th	,,	47	,,	,,	5	,,	6·5	,,	
5th	,,	33	,,	,,	7·5	,,	6	,,	
6th	,,	26	,,	,,	9·8	,,	5	,,	
7th	,,	22	,,	,,	11·5	,,	4·8	,,	

The differences seen on comparing this table with that given above[1] are trifling. They lose all importance when we take into account that the number of ripe proglottides in the second worm is about thirty less than in the first. Thus we see here, as in *Tænia saginata*, that the liberation of the ripe proglottides, apart from their separation in lengths, determines many individual and temporary differences. On the whole, we may credit *Tænia solium* with about 850 joints, which is tolerably harmonious with Küchenmeister's result, who counted 825 joints in a *Tænia* 5 yards 2 inches long. In this calculation a portion of the neck 6 lines long is left out of account, as "unsegmented."

The above-cited experiments (p. 496) show with considerable exactness how long time must elapse before the first joints are liberated. In the case observed by me, the patient voided the first joint two months and a half after the introduction of the bladder-worms, in the case observed by Vogt and Moulinié, the first joint appeared in the course of the third month. On the basis of these observations we may conclude that *it requires an interval of from eleven to twelve weeks to bring the development of the worm to completion.*[2] Küchenmeister[3] agrees thoroughly with this, and notes that when he has succeeded in expelling the whole worm except the head, the return of the proglottides may be certainly looked for in about ten or eleven weeks. The various stages of progress within this period are unknown. I can only note that in one case with which I was well acquainted, a tape-

[1] By an arithmetical error in the first edition of this work, the total number of joints was underrated, being stated at 749.

[2] In the first edition of this work, with fewer data, I approximately estimated the period at from three to three and a half months.

[3] "Parasiten," second edition, p. 90.

worm 90 cm. long, with proglottides just mature, was expelled exactly four weeks after an unsuccessful attempt at expulsion, which left only the head remaining.[1]

As to the age to which the worm may attain, we have here no greater certainty than in the case of *Tænia saginata*. This much, however, is beyond doubt, that the hook-bearing tape-worm may persist for a long series of years—perhaps for fifteen or twenty, or even for several decennia—but for how long is uncertain. In all these cases, there is always the possibility that the old inmate has been unconsciously replaced by a successor.

As a rule the parasitism of the worm ends by its expulsion from the host *in toto*. Whether dead or living, it is quite the same for the host, the expulsion takes place when the worm is no longer able to resist the pressure of the chyle or of the intestinal muscles. We have already noted in connection with *Tænia saginata* that the worm may under certain circumstances remain in the intestine for a while after death, until it falls to pieces or becomes mummified. The worm-mummy there described (Fig. 273) could be referred with some certainty to *T. solium*.

Malformations.

Malformations, properly so-called, are much less frequent in the hook-bearing tape-worm (the case is different with the bladder-worm) than the hookless *Tænia saginata*. I have only seen one instance. This was a proglottis with two symmetrical sexual openings and genital ducts—an abnormality which we have already noticed in *T. saginata* (p. 471).

On the other hand, here and there, six-rayed individuals occur. Krause[2] mentions a *Cysticercus cellulosæ* with six suckers, found in the brain of an idiot, and Zenker found on dissection of a tuberculous patient fourteen immature specimens of *Tænia solium*, one with six suckers and twenty-eight hooks. The adherent worm, which measured 46 cm., corresponded in respect of the prismatic form of its proglottides, and the position of the genital openings on the median ridge, with the analogous malformations of *T. saginata*.[3]

1 This worm showed in lengths of 25 cm.—350, 128, and 69 joints, and including the last 33 joints, which occupied 15 cm., had in all 580 joints. The largest joints measured 5 mm. long by 4·8 mm. broad, and were almost square, but still without embryos. The gradual growth of these joints may be expressed by the ratios 1·8 : 2·5 : 3·4 in width, to 2 : 3·6 : 4 in length, these being the dimensions in millimetres, both measured at the ends of the first three portions of 25 cm.

2 *Göttingen Nachrichten*, No. 18, 1863.

3 Heller, *loc. cit.*, p. 594 (Eng. transl., vol. vii., 709).

We will afterwards consider the malformations of the bladder-worms which are specially seen in those specimens found in the brain of man.

Organization of Tænia solium.

Sommer, "Ueber den Bau und die Entwickelung der Geschlechtsorgane von Tænia mediocanellata und T. solium," *Zeitschr. f. wiss. Zool.*, Bd. xxiv., p. 499, 1874.

The worm is distinguished not only by the size and general form of its jointed body, but also by the shape and structure of its component parts. Whether one examine a head or a proglottis, there can be no possibility of confusing it with *T. saginata.*

The Ripe Proglottides, which, in contrast to those of the last species, are very seldom liberated singly, present characters even more striking than the head, which requires for diagnostic purposes to be examined with the microscope, or at least with a lens. The flat form and the small quantity of parenchyma are at once evident when we press the proglottides between two glass slides and hold them against the light, or when we dry them on an even surface.

It is, however, the structure of the uterus which in reality determines our decision, for although we have also the shortness of the joints and their delicate transparent nature to help us, these characters are too deceptive to be implicitly relied upon.

In general, the ripe uterus of *Tænia solium*, with its few lateral branches, and the loose nature of its ramification, gives one the impression of being somewhat reduced and spare. This is specially evident on comparison with *T. saginata.* On the whole, the general appearance is the same, in so far as we have to deal with a median stem and with lateral branches. But the median stem is shorter, corresponding with the shorter joint, and the lateral branches are further separate, amounting hardly ever to more than nine on either side, and usually only to seven. I have not observed that they alternate irregularly as Sommer says. In fact they seem to me to be very symmetrical, except when neighbouring branches interlace, and when a lateral branch—sometimes indeed every alternate one—becomes abortive. The interlacing of these lateral twigs is on the whole much more abundant than in *T. saginata*, and more tree-like, so that the main branch is often turned from its transverse direction, and the secondary branches often come to have a somewhat longitudinal course, with exception of those at the ends, which are spread out like a fan. This is always the case with the anteriorly directed ramifications of the principal branches, which from their large size, regular distribution and shortness, exhibit

an almost comb-like structure. The same is often noticed in the distal off-shoots of the last lateral branches, but in their case this structure is less striking, partly because their number is more limited, and partly also because the associated lateral branches turn aside very regularly from their transverse position, and run in a curved direction towards the posterior angles. Otherwise they are scarcely to be distinguished from the others. The space marked off by them has the form of a flat, obtuse-angled triangle, and very generally contains at its angles the remains of the shell-gland. After what has already been said regarding the connection of the uterine structure with the state of general organization, it hardly needs to be expressly mentioned that in the proglottides of *T. solium* the ramifications of the uterus are much farther from the edge posteriorly than anteriorly. The transverse anastomoses of the lateral vessels limit the further distribution of the uterine branches.

Fig. 289.

Fig. 290.

Fig. 289.—Two segments of *Tænia solium* with branched uterus. (× $3\frac{1}{2}$.)

Fig. 290. — Proglottis of *Tænia solium* with slightly branched uterus. (× 2.)

Although the uterine branches are, as a rule, wider than in *Tænia saginata*, and are also not unfrequently swollen into a club-like shape, the number of eggs contained by the joints is smaller. Thus it appears that both in respect of the fertility of the individual segments as well as of the general character of the chain, *T. solium* is far behind *T. saginata* in its economic relations. This disparity is sometimes very marked in individual specimens; for (as is shown in the above picture of a very unfruitful joint, Fig. 290) there are some tape-worms whose lateral branches neither attain their normal length nor ramify as usual, but remain more or less abortive.

Although Weinland asserts that he once found proglottides like those depicted above in a hookless *Tænia*, we may safely assume, on the ground of later investigations, that they never originate from *T. saginata*. Whenever the associated worm has been investigated, its head and the formation of its joints have always proved it to be *Tænia solium*.

The head of the species, as has been repeatedly noted, differs from that of *T. saginata* chiefly in the possession of a hook-apparatus; but this difference, although the most important and the most striking, is by no means the only one. Other peculiarities of the species are

found in the size and form of the head. In accordance with the smaller proportions of this worm, its size is considerably less (the average hardly amounting to more than 1 mm.), and its form is more nearly spherical, for the back of the head is more markedly contrasted with the straight part of the neck, and the apex, situated on the rostellum, generally projects like a dome, 0·36 mm. high. The form of the apex is, however, subject to great variations, according to the state of contraction of the rostellum, so that it is sometimes more or

FIG. 291.—Head of *Tænia solium.* (× 45.)

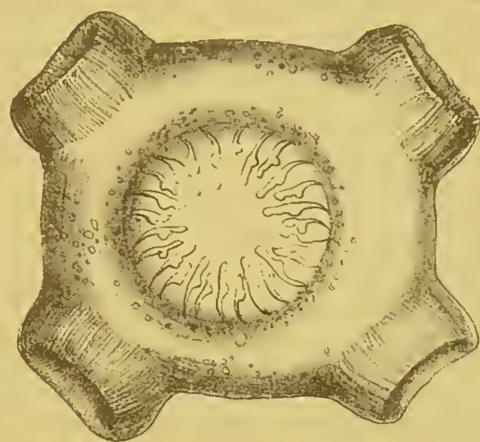


FIG. 292.—Apical surface and circle of hooks of *Tænia solium.* (× 80.)

less deeply sunk in the wall of the head, and at other times elevated into a conical or plug-like proboscis. After what has been already noted regarding the significance of the rostellum and the motor mechanism of the hooks, it is easy to see that each of these differences in form is associated with a particular attitude. If the apex be retracted, the hooks are so placed that their points are directed forwards, pretty much in the longitudinal direction of the body. If the apex be still more deeply sunk, the hooks sometimes come to have their points resting together at a common centre. Thence, by the progressive protrusion of the apex, they gradually become directed so far backwards, that the concavity, with the now posteriorly directed points, is in contact with the sides of the protruding extended proboscis.

The size of the suckers corresponds to the smaller development of the head, for they only measure 0·4 to 0·5 mm. But in spite of this they are generally more prominent than in *T. saginata.* The flattening of the head is, however, less striking, for the sagittal diameter is only a little less than the frontal (Fig. 292).

On a former occasion, I have described the very various positions which are characteristic of the suckers of *Tænia solium* (p. 513). They may be moved singly or in pairs, opposite to each other, or the whole four may be raised up like arms, extend in different directions, and then contract. Displacements of the rostellum are generally associated with these movements, and indeed so constantly, that there is an unmistakeable connection between these various actions. This is very marked when the suckers feel about in front as though trying to fix themselves to some object situated in front of the head. As often as this motion takes place, the apex is observed to sink in, and to remain for a time in this position, before again protruding and allowing the hook-apparatus to unfold itself.

When we remember that this is the way in which the suckers attach themselves to the wall of the intestine, and press the front of the head against it, it will be seen that on the protrusion of the apex the points of the hooks must press into the wall of the intestine and penetrate the deeper the further they are removed from the apex; and as the apex at the same time, by the flattening of the formerly cup-like rostellum, drives the points of insertion of the hooks further from each other in a radial direction, the fastening is of course made all the stronger, sufficient in fact to keep the body in its position without the help of the suckers, and to present the necessary resistance to the pressure of the chyle.

A separation may take place when the worm is not fixed too deeply by a rupture of the intestinal villi, in consequence of the tension exerted on the body of the worm, and thence transferred to the extended hooks. It may happen, too, that the hooks straighten themselves up and relax their hold of the surrounding tissue.

The manner in which the rostellum is concerned in all these processes need not be again discussed, after our former remarks regarding the motor mechanism of the hooks (p. 401). It is equally unnecessary to explain the structure of the rostellum and the associated muscular disc, or to discuss the nature and mechanism of the suckers (see p. 395). In regard to all these parts, we need only remark that they do not differ in any respect from the usual conditions of the cystic tape-worms. It is true that Nitsche attempted to establish certain peculiarities in regard to the structure of the muscles of the circlet of hooks in *Tænia solium*, but this was probably due to the unsatisfactory nature of his material. In reality the structure of *T. serrata* is exactly repeated in *Tænia solium*. Especially is it impossible to regard the pouches intended for the reception of the roots as a special characteristic of *Tænia solium*, although they were the occasion of Küchenmeister's proposal to renounce the apparently

meaningless name of *Solium* and to call the species *T. hamoloculata.* On the contrary such pouches are always found in the hook-bearing *Tæniæ*, for the hooks never merely project, but always have their roots sunk in the external coverings of the head. After the falling out of the hooks (which often takes place very soon after the removal of the worm from the intestine, and especially if it be placed in water), these pockets are, it is true, less distinct and striking than in *Tænia solium*, though this is only the case when the apical region is permeated with a black pigment, as indeed it generally is. In such specimens, the hook-pouches appear as gaps in the pigment, and are very noticeable even on superficial examination. But, on the whole, this pigmentation is less frequently observed in *T. solium* than in *T. saginata.*

The Circlet of Hooks and the *Hooks* themselves must now receive our attention.

As in the related forms (with the exception of *Tænia acanthotrias*), the circlet of hooks in *T. solium* is double (Fig. 292): in other words, although the hooks all have their points on the same circular line, they do not form one, but two successive rows, one anterior to the other. The hooks of the anterior row are larger than those of the posterior, and are fixed to the rostellum somewhat above the lateral border, so that their centre of motion is not so far from the common centre as is the case with the smaller, more peripherally situated hooks. Besides these differences in position, there is also a slight difference in the formation of the roots, for those in front, being situated on a less curved surface, have flatter bases than those behind.

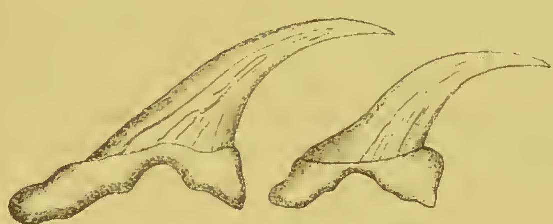


FIG. 293.—Larger (anterior) and smaller (posterior) hooks of *Tænia solium.* (× 280.)

The number of and distance between the hooks are the same in both rows, and the smaller ones always occupy the spaces between the larger, so that large and small hooks are in regular alternation. The above-mentioned differences in the size of the hooks depend mainly upon the different lengths of the posterior root-processes, which in the large and small hooks have the ratio of 3 : 2. But these are not the

only differences that prevail. In the small hooks the anterior process is broader at the end than in the larger ones, and is almost two-lobed the claw is also shorter and narrower, and more bent at the base. The considerable thickness exhibited by the basal portion of the larger claw is due mainly to the fact that it is, so to speak, prolonged further into the posterior process than is the case in the small hooks. To this circumstance is also due in great measure the considerable length of the posterior process, which has already been noticed in the hooks of the anterior row. The solid portion of the process, which is generally marked off from the base by a slight groove, does not measure much more in the anterior hooks than in the posterior ones.

All these, however, are features which *Tænia solium* shares with most of the other large-hooked cystic tape-worms. Much more characteristic is the above-mentioned compressed and rather stout form of the hooks, which, however, can only be rightly appreciated on comparison with those of related species. Another slight difference is that in both small and large hooks, and especially in the latter, the base of the posterior process is somewhat emarginate in the middle. Certain other peculiarities, in regard to the size of the hooks, serve more firmly to establish the diagnosis. The distance of the point of the claw from the end of the posterior process is in the large hooks 0·167-0·175 mm., and in the small ones 0·11-0·13 mm. (in *T. serrata* 0·25 and 0·14 mm., and in *T. crassicollis* 0·39 and 0·16), while the end of the anterior process is about as far from the point of the claw as it is from the end of the posterior root-process—that is to say, 0·09-0·1 mm. in the larger hooks, and 0·064-0·07 mm. in the small ones.[1]

The number as well as the size of the hooks varies very much in individual cases. The extremes are somewhat wide apart, for while the smallest number is twenty-two, the largest, according to Davaine, is thirty-two. Most frequently twenty-six or twenty-eight hooks are found, half of them small and half of them large, so that the uneven numbers seem excluded. Bladder-worms which are developed at the same time beside each other appear to exhibit for the most part either one or other of these two numbers.

The malformations occasionally found in the hooks have already been noticed (see p. 398); although, as I see no special mention has been made of this species, yet it was for the most part this species, or rather the corresponding bladder-worm, that I had in view in making

[1] Further measurements are given by Küchenmeister ("Parasiten," first edition, p. 178). I omit these, because I think that the points from which the measurements are taken are much too uncertain to render the size given of much value. In comparing his results with the above statements, I will only mention that his measurements are in all cases somewhat larger than mine.

those remarks.[1] Whether there are also adult tape-worms with malformed hooks is doubtful, since the imperfect development of the hook-apparatus would hardly permit a long enough residence in the intestine to allow of the full development of the worm.

The Structure of the Joints calls for little addition to our previous description, except as regards the sexual apparatus. Everything else has already been mentioned in one place or other. We know, for example, that *Tænia solium* is far from possessing the powerful musculature of *T. saginata.* We are also acquainted with the fact that the four longitudinal vessels originally present are reduced to two before the appearance of the sexual organs, and that they then run throughout the whole length of the chain in the form of two wide stems, which are always connected at the posterior border of each joint by a transverse anastomosis. It is true that for a time the four stems may be seen near each other, but they are no longer arranged in pairs on the two flat surfaces, as in the head, but are all on the same plane and close together. The change of position takes place at the beginning of the neck, and is evidently caused by the marked flattening of the segmented body, which no longer admits of the former distribution of the vessels. In consequence of this, each of the two narrow sides has an outer and an inner vessel, so arranged that the vessels of the ventral female surface become the external, while those of the dorsal male surface come to lie internally. It is difficult to say by what influences the two inner vessels have become dwarfed, but this is very probably due to the peculiarities of the position of the worm. Moniez conjectures that the cause of the diminution is the development of the sexual organs, which might, indeed, have some effect on the adjoining parts; but it is demonstrable that they only attain their complete development at a time when these vessels have already disappeared.

In regard to the calcareous corpuscles, we need only remark that they are upon the whole sparsely distributed, and less marked than in the related species, especially *T. saginata.* It appears, however, as though all specimens were not alike in this respect. They also exhibit many variations in size, but, as above mentioned, seldom exceed 0·012 mm.

The Reproductive Organs exercise a marked influence upon the general form and organization of the body, just as in *Tænia saginata*

[1] In support of the assertion which I made at that time, that there are some bladder-worms in which the circlet of hooks is not developed, I refer to the case described by Lewin (*Annalen des Charité Krankenhauses*, ii., p. 167 : Berlin, 1875), who found a hookless bladder-worm from a pig, which possessed, instead of the rostellum, and evidently as a representative of it, "an extra fifth sucker."

—an influence compared with which that of the calcareous corpuscles, vessels, and muscles is quite insignificant. What we have already said in this respect of *Tænia saginata* is true, even down to details, of *T. solium*, which so closely agrees with it both in structure and development that, with some slight alterations, the former description might be adopted almost word for word.[1] Accordingly, it is unnecessary to describe minutely the reproductive apparatus of this species. It will be sufficient for our purpose to emphasise the differences which exist between the two forms; and in regard to any other points, to refer to what was said of these organs whilst treating of *T. saginata.*

These differences arise in great measure from the fact, already often mentioned, that in its vegetative powers *Tænia solium* falls far short of *T. saginata.* Thus, not only is the form of the uterus influenced by this fact, but the whole of the reproductive apparatus.

This is especially evident from the fact that the sexually mature joints of *Tænia solium* are considerably smaller than those of *T. saginata.* They exhibit hardly more than half the diameter of those of the latter, being not more than 4·5 to 5 mm. in breadth, and 2·5 to 3 mm. in length. These differences in size of course find expression also in the individual parts of the reproductive apparatus. All the dimensions are smaller, the sexual pores less prominent, the testes considerably fewer in number, and the cæcal tubes of the yolk-gland, as well as of the germ-glands, are less branched and less compactly aggregated. Even the form of the germ-glands corresponds to the generally smaller space. Their longitudinal diameter is less than in *T. saginata*, and the round discoid form of the latter is exchanged for a transversely oval one. This is true especially of the smaller lateral lobe which lies under the vagina, on the right or on the left of the middle line, according to the position of the genital pore. But on the same side above the vagina, and in the angle open in front, which the descending limb forms with the uterus, there is always (and not merely occasionally, as I stated in the first edition of this work) a group of ovarian tubules. These are

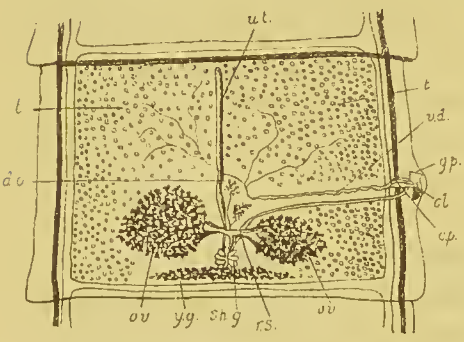


Fig. 294.—Reproductive organs of *Tænia solium* (× 10). *g.p.*, genital papilla; *cl.*, cloaca. Male organs.—*t.*, testes; *v.d.*, vas deferens; *c.p.*, cirrhus-pouch. Female organs.—*ov.*, ovary; *y.g.*, yolk-gland; *sh.g.*, shell-gland; *r.s.*, receptaculum seminis; *ut.*, uterus; *d.o.*, detached portions of ovary.

[1] Indeed, the account given in that place of the reproductive organs of *Tænia saginata* was largely borrowed from the description which I gave in the first edition of this work of the characters of *T. solium* (p. 261 *et seq.*).

entirely absent in *Tænia saginata,* and therefore furnish a very welcome diagnostic characteristic for the young proglottides of *T. solium.* The tubes are situated upon a somewhat long and slender canal, which branches off, at the side of the uterus, from the common transverse oviduct, and ascends in an anterior direction. According to Sommer, these form a peculiar "intermediate" lobe of the ovary, but I think that it is more natural, and also more in accordance with the usual structure, to regard them as an isolated and separated portion of the neighbouring lateral lobe.

By its depressed form and much extended sides, the yolk-gland repeats the proportions of the ovary, but in consequence of its more simple contour its peculiarities are less striking.

I need not dwell long upon the structure and connections of the various reproductive organs. What has been said in this respect of *Tænia saginata* is also true of *T. solium.* At the most, there is only a small difference between them, inasmuch as the canal connecting the uterus with the shell-gland has in *Tænia solium* a relatively greater length; hence the uterus appears of course still shorter.

The smaller size of the reproductive apparatus makes it quite possible that its development may take place over a shorter stretch of joints. Although the first rudiments of the sexual organs appear in both at pretty much the same distance behind the head, or about the 200th joint, the period of sexual ripeness, in so far as it is announced by copulation, and by the commencement of the transference of eggs into the uterus, occurs at parts of the body which are at least 150 to 180 joints distant from each other. Instead of being at the middle of the seventh hundred, it is in *Tænia solium* in the second half of the fifth hundred that the first eggs are found in the uterus. At the former of these places, that is, where the sexually ripe joints were found in *Tænia saginata,* the eggs of *T. solium* have already undergone a great part of their development. The ramification of the uterus begins very soon after the 600th joint, while in *T. saginata* it only appears about the middle of the eighth hundred,—that is to say, at a place where *Tænia solium* already exhibits ripe proglottides.

The peculiarities of the processes which we have thus shortly summarised are exactly the same as in *T. saginata,* so that it is not necessary to enter into further particulars regarding them. To do so would be only to repeat what has already been said (pp. 445, 446). The specific peculiarities of *Tænia solium* become conspicuous only in the last phases, when the uterus begins to branch, and indeed find expression only in the fact (Figs. 295 and 296) that the lateral branches are fewer in number. So long as the proglottides are broad and short, the latter are of considerable length, and slender in form.

At this time they are also destitute of the numerous short off-shoots, which only appear when the commencing longitudinal extension diminishes the transverse diameter of the worm, and when the transverse canals begin to shorten; and it is only at this time that the formerly dichotomous branchings assume by anastomosis the form so characteristic of this species.

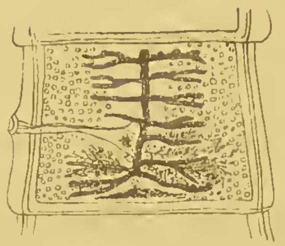


Fig. 295.—Half-ripe joint of *Tænia solium*. (× 2.)

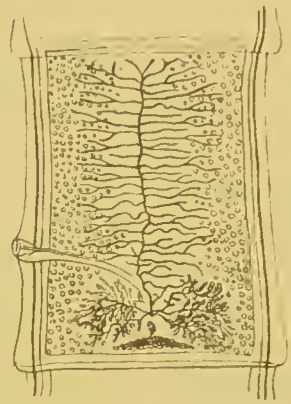


Fig. 296.—Half-ripe joint of *Tænia saginata*. (× 2.)

What I have observed regarding the embryonic development of *Tænia solium* is in close correspondence with that of the related forms. In the half-ripe eggs, besides the embryo, or the ball of cells which becomes changed into it, there are three large nucleated cells, with granular masses filling up the interspaces between them. These structures are enclosed along with the embryo in an envelope, which is often tailed, and are still to be found when the embryo has become surrounded by its shell. Afterwards most of the cells are destroyed, so that there only remains within the shell-bearing embryo a viscid fluid abounding in granules. This reminds one somewhat of the albumen of a bird's egg, and, like it, is surrounded by a kind of shell, namely, the enveloping membrane. But in the ripe proglottides both the albumen and membrane have generally disappeared, or rather have been resolved into a pulpy substance, which, along with the shell-bearing embryos, form the so-called "eggs of the proglottides," which fill the interior of the uterus. The shell of the embryo is, as in *Tænia saginata*, thick and firm, of a brownish colour, and covered with countless little rods, but of a rounder shape. Its diameter amounts to 0·03 mm., while that of the simple embryo is not more than 0·02 mm.

Fig. 297.—Eggs of *Tænia solium*, (*A*) with and (*B*) without primitive vitelline membrane. (× 450.)

Occurrence and Medical Significance.

1. The Adult Tape-Worm.

As is well known, *Tænia solium* is one of the intestinal worms which are found exclusively in man. Von Siebold certainly asserts that he reared tape-worms from the *Cysticercus cellulosæ* of the dog,[1] but as he (with Pallas and other older helminthologists) regarded the human tape-worm as identical with the cystic tape-worms of the dog, his results are of course no longer valid.[2] Other investigators, who knew how to distinguish *Tænia solium* from the large-hooked tape-worms of the dog, have never succeeded in rearing the bladder-worm of the pig in the intestine of the dog, although such investigators as Haubner, Küchenmeister, Heller, and myself made experiments on a considerable number of these animals. Just as little success has attended experiments with other mammals, such as pigs and martens (Leuckart), cats, rabbits, guinea-pigs, and apes (Heller).

Of course, even in man, every bladder-worm does not grow into a tape-worm, nor even every one of those that enters the stomach uninjured—that is to say, with uninjured head. Küchenmeister estimates the loss in the above-mentioned cases at about 50 per cent., but this estimate has only an uncertain value, since the result must vary much in different cases, both with the more or less thorough mastication and with the nature of the gastric juice.

The hypothesis of a special predisposition to the tape-worm, which was formerly held on the ground of certain statistical facts, is now abandoned. In every case the occurrence of *Tænia solium* depends upon a further development of the *Cysticercus cellulosæ*. Whenever the latter gets into the human intestine in a condition capable of development, there is not only the possibility, but the probability, of this further development, and this is quite independent of the age or sex of the individual who is infected. The frequency of the worm is always determined by the opportunities given for this reception, and will increase, of course, in proportion as it is favoured and facilitated by the habits and mode of life.

As might be supposed from such a state of affairs, *Tænia solium* always occurs where the pig is reared and eaten as a domestic animal, and is most frequent where (*ceteris paribus*) the breeding of pigs is most common. So that *Tænia solium* is probably, like *T. saginata*, cosmopolitan. It is, however, doubtful whether it is so universally

[1] "Band- und Blasenwürmer," p. 87.

[2] This explains the great dissimilarity, in v. Siebold's case, between the administered bladder-worms and the tape-worms which he afterwards found,—a fact which even at that time gave rise to the conviction that the dog was but little adapted for rearing the bladder-worms of the pig.

and regularly distributed as the latter; for the pig is not only on the whole a much less common source of food than the ox, but in many countries, and expecially in those of the Torrid Zone, it is either never or only occasionally and exceptionally eaten. I may recall in this connection the Abyssinians, who loathe swine's flesh, and are therefore exempt from *Tænia solium*—that is to say, from Rudolphi's hook-bearing form.

Owing to the confusion which has prevailed until our own day regarding the diagnosis and nomenclature of the two chief tape-worms found in man, it is impossible to determine rigidly their range of distribution. But it is at least certain that *Tænia solium* is found, not only in Europe and in North America,[1] but in Australia, India, Turkestan, and Japan, although in the last-named localities (in Japan, according to a communication of Prof. Baelz in Tokio, and in Turkestan, according to Fedschenko) it is much less frequent than *T. saginata*. Even in Europe it is well known that there are many countries (p. 480) in which *T. saginata* predominates, while others are more infested by *T. solium*. So far as we know, the latter is most frequent in certain districts of England and Germany—such as Thuringia, Saxony, Brunswick ("around the Harz," as Göze has remarked), Westphalia, Hesse,[2] and Württemberg,—in all of which the breeding of pigs is common, and much pork is consumed. As we have already mentioned, its occurrence has of late, according to all appearance, been much less frequent. In Leipzig, for example, where *Tænia solium* used to be frequently observed, it is now difficult to find a specimen of it; and Krabbe writes to me that in Denmark the per-centage has, within the last ten years, diminished from 53 to 20. I need hardly add that this decrease is a triumphant result of our helminthological investigations. The relations of *Tænia solium* to the *Cysticercus cellulosæ* have become more widely known, and the flesh of the pig, which also harbours *Trichina*, is more carefully inspected, and less frequently

[1] Regarding the occurrence of *Tænia solium* in North America (among negroes and white people), see Weinland, "Tape-Worms of Man," p. 39: Cambridge, U.S.A., 1858.

[2] Of fifty-seven cases of tape-worms in Giessen known to me during the first year of the seventh decade of this century, forty-five were *Tænia solium*. Müller also reports in his "Statistik der menschlichen Entozoen" (see p. 151) that of twelve cases of tape-worm found in the hospital at Dresden, ten were due to this worm, and in Erlangen only seven out of ten. For the sake of comparison, I may add that Krabbe in Copenhagen found *T. solium* fifty-three times out of a hundred cases, Giacornini in Turin four times out of eight, Grassi in Milan three times out of twenty-five cases, and Marchi in Turin once out of thirty-five. *Tænia solium* is thus much less frequent in Italy than in the middle and north of Europe; but of course this does not exclude the possibility of its being found in greater numbers in particular places. Sangalli, for example, reports that this is the case in Rome. Regarding the occurrence of the tape-worm in Italy, see Grassi—"Contribut. allo stud. dell' Elmintolog.," *Gaz. med. Ital.-Lomb.*, t. i., p. 4, 1879; and for Krabbe's reports, see his *Ugeskrift for Laeger*, Bd. vii., No. 7, 1869.

eaten raw, and all this has tended to restrict the frequency of the tape-worm. For the calculation of the per-centage we can only rely upon the reports of Müller, according to which *Tænia solium* was found nineteen times in 3814 *post-mortem* examinations (in Dresden and Erlangen)—that is, about once in 200 examinations, or 0·5 per cent. In Dresden its occurrence was somewhat more frequent than in Erlangen.

After what we have said on a former occasion regarding the transference of *Tænia saginata*, it is easy to see that the occurrence of *T. solium* is by no means exclusively determined by the consumption of flesh, but quite as much, and indeed almost more, by the condition and preparation of the meat. And the more frequently the latter is eaten in a raw or half-raw condition, in consequence of local or individual custom, the more does the danger of infection increase.

It is true that, upon the whole, pork is much less frequently eaten raw than beef, and that it is also less frequently ordered for dietetic purposes; but in certain districts, and especially where there is a large manufacturing population, it is a favourite dish in the form of mince-meat, which is merely salted and peppered. Speculative butchers even prepare this mince-meat from measly flesh, which thus loses its suspicious appearance, but almost none of its danger; for, as we have seen (p. 382), the bladder-worm heads are alone sufficient to transmit the tape-worm.

For the same reason, the prepared meats bought in small portions in butchers' shops (and particularly sausages and ham) are by no means so harmless as at first appears. They probably often form the vehicle of *Tænia solium*, and all the more so, since butchers are accustomed to remove the free-lying bladder-worms with the knife, and perhaps with the very same one which is afterwards used to chop up the meat.

Further, when we consider the great adhesiveness possessed by the bladder-worms and their heads, on account of the damp nature of their surface, it will be seen that the possibility of a transference is by no means limited to such a case. The possibility is always present wherever raw pork is stored, and the transmission may be effected by the most manifold objects, and that all the more easily since, as is well known, the bladder-worm of the pig is found very frequently, and usually in great numbers. Nor are the worms transferred in food only. Under some circumstances, even the hand is quite sufficient, especially since, to quote the common saying, there is but a short road from it to the mouth. Cases have even been heard of in which not only children, but even adults, have picked up and swallowed single bladder-worms in the kitchen.

But it is not necessary to quote these cases of perverse gluttony in order to prove that the bladder-worms of raw pork, just like those of beef, frequently find an entrance into man and produce the tape-worm. Statistics also abundantly show that those persons whose position and vocation oblige them to handle raw meat, or to taste little portions before it is perfectly cooked, are as often afflicted by *Tænia solium* as by *T. saginata.*[1] Of Krabbe's fifty-three cases no fewer than forty-two belonged to the female sex, and only eleven to the male.[2] The occupation and position of these persons could not always be ascertained, but so far as it was possible to do so, it appeared that half of the female patients were housemaids and kitchen-maids. So far as the age could be learned, three-fourths of all the patients were between twenty and forty. In children under ten (and Krabbe observed the worm even in some three or four years of age) the two sexes seemed equally liable.

The circumstance that Krabbe's lists contain a relatively large number of Germans, is explained by the author in a letter to be due to the fact that the latter, even in foreign countries, adhere to their custom of eating raw flesh and fresh sausage, and of usually procuring the latter in small quantities from the butcher's shop. The same is asserted of the Germans in Paris, among whom the tape-worm also seems to occur with unusual frequency.[3]

The counterpart to this is furnished by the fact that among thirty-five *Tæniæ* which Marchi collected in Florence within a certain time, he only found a single *T. solium,* although during that time no fewer than 13,000 measly swine had been imported and eaten.[4]

The almost entire immunity of the inhabitants of Florence from *T. solium* is due, as is shown by Pellizzari, to the circumstance that with them pork is never eaten raw like beef (from which they get *Tænia saginata*), but is always carefully cooked. By cooking the bladder-worms are almost sure to be killed, and at any rate much more frequently and thoroughly than the *Trichinæ,* which, as is well-known, only die at a temperature of about 60° C. (140° F.), while the former generally perish at 47° C. and 48°, and hardly ever survive 49° (120° F.).

1 The similarity of the conditions of infection also explains the fact that both kinds of tape-worms not unfrequently occur at the same time in the same individual. Such cases have been observed by Krabbe, Müller, and Heller; by the latter in a butcher.

2 Müller's reports, notwithstanding the small number of cases, also leave no doubt that *Tænia solium* is more frequent in women than in men.

3 Lancereaux, *Arch. génér. méd.*, t. xx., p. 553.

4 Pellizzari and Cobbold, "Parasiti interni degli Animali domestici," Trad. dal Tommasi, Append., p. 172. On the authority of this, Küchenmeister states that 13,000 kilos of measly pork are consumed yearly in Florence.

The most thorough investigations regarding the power of resistance of the bladder-worms of the pig are due to Perroncito. Although at first inclined to the opinion that it required a temperature of at least 125° C. (257° F.) to render the bladder-worms harmless,[1] he was afterwards enabled, by means of a more exact method of investigation, to establish that the latter are certainly killed when the temperature of the surrounding fluid reaches 50° C., or even below that, and when the worms remain in it longer than a minute.[2] What impelled Perroncito to these renewed researches was the opposition to his first results on the part of Pellizzari, who, like Lewis and Cobbold, had fixed the fatal temperature at about 60° C.

The difference between these results is explained in this way, that the experiments on which they are founded were made sometimes on large masses of flesh, sometimes on the isolated bladder-worms, where the surrounding temperature would of course affect the actual objects with varying rapidity and completeness.

To fix the absolute power of resistance possessed by the bladder-worms, it is best to take the isolated worms, as Perroncito did in his later experiments. He placed them on Schultze's warm stage, and observed the effects of increasing warmth. While the bladder-worms at low temperatures (under 16° to 20° C.) usually remain motionless, after passing above 30° to 35° C., more or less lively contractions of the body as a whole, and particularly of the suckers and proboscis, are observed. The movements become still more energetic at a temperature of 42° to 45° C., but then suddenly stop, in some cases at 45° C. or 46° C., or only at 48° C., and do not begin again even if the worm be gradually cooled down to the temperature of the air, and allowed to rise again. Only in one case did a *Cysticercus* survive a temperature of 49° C.; but it became motionless at 50° C.

Perroncito showed distinctly that the motionless state is in reality death, not only by the use of the warm stage,[3] but by proving experimentally "that such overheated bladder-worms had lost their power of development." One of his students, a young Dr. M., swallowed on two different occasions (January and March) a bladder-worm which had been thus heated up to 50° C., and remained free from tapeworm.[4]

In order to ensure the death of the bladder-worm in cooking, a

[1] "Della panicatura degli animali," *Ann. R. Accad. Agricolt. Torino*, t. xv., 1872.

[2] "Sulla tenacita di vita del Cysticerco della cellulosa," *ibid.*, t. xxx., 1876 (abridged in Moleschott's *Unters. zur Naturlehre*, Bd. ix., No. 37), and "Della grandine e panicatura nell' uomo e negli animali," *ibid.*, t. xix.

[3] The attempt to prove death by the "inhibition method" yielded but doubtful results, so that we may omit it.

[4] "Sulla tenacita, &c.," p. 21.

higher temperature and a longer exposure to it are necessary. The flesh must be boiled or roasted till it is "done through and through." No bladder-worm can survive the coagulation of the surrounding albumen, or the decolorisation of the blood, but half-cooked flesh contains numerous living bladder-worms.

The process of smoking and pickling, if rightly conducted, may also render the bladder-worm harmless. Weinland, indeed, speaks of a rumour current in Boston that the English soldiers during the Crimean war rejected the cured ham sent them from home, since it infected them with tape-worm; but this is contradicted by the fact that the bladder-worms can hardly survive the death of their host more than a few weeks.[1]

As to ham properly prepared from measly flesh, my experiments, which were detailed in the first edition of this work, and which were the first on the subject, have proved its harmlessness. As I then pointed out, the fluid in the bladder gradually disappears by evaporation during the smoking. The body collapses, and, after a short time, acquires, like the head, a turbid character. Even in fresh ham, bladder-worms so altered never exhibited any symptom of life, even when I transferred them into the stomach of a newly killed animal, and surrounded them with the moist warmth of the incubating apparatus. This was equally unsuccessful in the case of older ham, in which the bladder-worms had shrivelled up into knots of the size of a large pin-head.

Küchenmeister arrived at similar results in the experiments which he has lately conducted along with Siedamgrotzky in the Dresden Veterinary College, but their cogency is weakened, inasmuch as the measly flesh (cured and smoked) was given to a dog, an animal not specially adapted to prove the vitality and developmental potency of bladder-worms from the pig.

Not only culinary treatment, but also decomposition of the flesh, soon puts an end to the life of the bladder-worm. In midsummer I have seen the bladders becoming flabby and turbid in eight days, while in autumn and winter they were alive and in motion (in moist warmth) after I had kept the measly flesh fourteen days in a space secured from frost, at a temperature of from 5° to 8° C.

Although the danger of infection by food prepared from pork is thus on the whole but slight, yet it cannot be denied that the popular methods do not always ensure the death of the inmates. This is especially the case with those dishes, such as cutlets and sausages, which are rapidly prepared. Such dishes serve to explain the presence of tape-worms in persons who have certainly never eaten raw meat.

[1] "Tape-Worms of Man," p. 36.

The occurrence of the bladder-worm in groups explains how the presence of several specimens of the *Tænia solium* within one host is much more frequent than was the case with *T. saginata* (the "ver solitaire"). Two or three of the former often live together in the same intestine, and from six to ten specimens are not uncommon. Sometimes the number is still greater,[1] as is proved by the cases of Kybuss, who within eight hours expelled twenty-five tape-worms from one patient; of Heller, who disentangled twenty-eight individuals from an expelled ball of tape-worms; and of Kleefeld, who actually observed forty-one chains existing simultaneously within one individual. The last subject had, it is expressly noted, eaten raw pork daily for four years, and had not even rejected what was measly.[2] Similarly Küchenmeister reports the case of a man who voided thirty-three *Tæniæ* at once. He was, as Küchenmeister remarks, "the sweetheart of a butcher's daughter, and often got bladder-worms to swallow from his love." I myself knew a case of a hysterical woman, who was ordered to eat raw flesh for dietetic reasons, and who expelled seventeen tape-worms on two occasions within eight days.

Jews, who eat no flesh of swine, of course remain free from *Tænia solium*, but are hardly less infested with *T. saginata* than their Christian neighbours.

With regard to the length of life and position of the worm, and with regard to the disorders due to its presence in the intestine, it is perhaps enough to refer to what we have already said about *T. saginata*. This difference ought, however, to be noted, that the phenomena of intestinal irritation, and the resulting nutritive and nervous disturbances, are very much less intense in *T. solium* than in the case of *T. saginata*.[3] We may, indeed, infer this from the fact that *T. solium* not only grows more slowly, and is as a whole not only shorter, but also much less muscular, and, therefore, that by its contractions the intestinal mucous membrane and its villi are less frequently and less intensely irritated. On the other hand, *T. solium* has, of course, in its circlet of hooks a weapon which is probably not without importance from a medical point of view. We know, indeed,

[1] I must leave it undecided whether Gmelin's report of finding 200 tape-worms together in one host is really based on fact (Linn., "Syst. nat.," ed. xiii., t. i., p. 6, p. 306).

[2] *Deutsche Klinik*, No. 16, 1853.

[3] Lewin has lately (*Ann. d. Charité-Krankenhauses*, p. 656, Th. ii., Berlin, 1875) asserted that the frequent disturbances of the nervous respiratory and circulatory functions occurring in tape-worm patients are not due to the tape-worm, but to the *Cysticerci* which likewise occur. But he forgets that these phenomena are much more constant and striking in the case of *Tænia saginata*, which has never yet been observed in the Cysticercoid state in man.

that by means of this weapon the worm may penetrate the intestine of its host, and thus occasion injuries which may under certain circumstances cause ulceration, and similar pathological conditions.

It is, however, only in its immediate effect on the intestine that one *T. solium* is of less account than one *T. saginata*. But *T. solium* very frequently occurs not solitary, but associated with several or even with many companions, and this very materially alters the state of the case, for not only is the irritation of the intestine and the loss of nutritive juice increased, but the adjacent worms occasion frequent movements by their mutual contact and pressure, and also roll themselves up into a ball.

In estimating the clinical importance of *T. solium*, we have to do not only with the troubles above referred to, but also with the fact that the embryos may develop within the human body as well as within the pig, and may thus, according to their position, occasion diverse pathological states, and may often endanger even the life of their host. Since the bladder-worms of *T. saginata* have never been found as yet in man, we must concede that, in spite of the probably less intense intestinal irritation, *T. solium* is by far the more dangerous species. The proglottides and eggs voided by the patient endanger not only his own health, but also that of his neighbours, so that the removal of the unwelcome guest is a pressing necessity. It would, indeed, be justifiable to have a sanitary law to the effect that the worm should be at once expelled, for the host is a source of danger to the community.

2. The Bladder-Worm.

Stich, "Ueber das Finnigsein lebender Menschen," *Annalen des Charité-Krankenhauses*, Jahrg. iv., p. 154 : Berlin, 1853.

Lewin, "Ueber Cysticercus cellulosæ und sein Vorkommen in der Haut des Menschen," *Annalen des Charité-Krankenhauses*, Jahrg. ii., p. 609 : Berlin, 1875.

Davaine, "Traité des entozoaires, &c.," second edition, p. 667 : Paris, 1860.

We have already noted (p. 511) that the disease caused by bladder-worms has been known for centuries. Apparently, indeed, the knowledge of these forms dates from remote prehistoric times, for the first mention of the bladder-worms of the pig (in the "Knights" of Aristophanes) refers to the then existing custom of examining the tongue of the pig, in order to detect the presence of the so-called χάλαζαι (grandines). Under these circumstances, the supposition seems not improbable that the prohibition of swine's flesh among Jews and other Oriental peoples had for the most part reference to the presence of bladder-worms.

We know, however, that the animal nature of the bladder-worms was not detected till towards the end of the seventeenth century, nor was it generally recognised till at a still later date (in consequence of the researches of O. Fabricius and Göze). Till then the bladder-worms were regarded as tumours, closely allied to the encysted and glandular tumours. In Oribasius and Aëtius we find it stated that Androsthenes compared them to tubercles, and that Aretæus compared measly pigs to people suffering from elephantiasis. The fact, known even in Aristotle's day, that new-born pigs had no bladder-worms, seemed quite to harmonise with the theory which sought to explain these structures as diseases.

Our knowledge of bladder-worms did not, however, attain any completeness till the genetic relation between them and *T. solium* was demonstrated. Then for the first time it was seen that the bladder-worm disease, which had been formerly referred to bad food, such as decomposing corn or acorns, or to infection and inheritance from one pig to another, always originated from infection with the eggs of the common hook-bearing tape-worm infesting man. Such an infection is greatly facilitated by the habits of the pig, which rejects neither human excrement nor water from the dung-heap, and by the fact that the joints of *T. solium* are always expelled with the fæces, and sometimes hang together in numbers even after expulsion. Thus it is explained that the bladder-worms of the pig are only rarely found isolated, but usually live in companies, and sometimes in such numbers that the flesh looks almost like frog's spawn. In the case of an animal experimented on by Haubner, there were in one piece of flesh about 17 grams in weight not fewer than 133 bladder-worms, so that, supposing the distribution uniform, the total number present in a mass of flesh weighing 20 pounds would be about 80,000. I obtained similar results from one of my experiments, in which I counted 250 bladder-worms in about 31 grams of flesh.

Cases of such abundant infection are of course rarer in nature than in experiment, but some might be cited where 15 grams of flesh contained about 30-40 bladder-worms, and where the total number of parasites might be estimated at from 12,000 to 20,000. The favourite situations of the worms are the breast and shoulder muscles, the tongue, the diaphragm, and the legs. The gullet, heart, and the subcutaneous tissue are also frequently inhabitated by bladder-worms, as are also the nervous centres and eyes, while the viscera are, as a rule, only rarely infested.

The symptoms of disease vary according to the situation and number of the bladder-worms. When they occur but sparsely, and are restricted to the muscles, they occasion hardly any disturbance.

In such cases they may be perceived even during life when they occur on the under surface of the tongue or inside the eyelids. But even in cases of abundant infection the worm is by no means always recognisable with certainty. Hoarseness and falling out of the bristles are indeed common, but they are neither certain nor constant, and are apparently only present when the laryngeal muscles and subcutaneous tissue are penetrated by the parasites. In extreme cases they produce a definite cachexia, which, in consequence of continued and aggravated disturbance of the nutrition, may finally end in death. When an excessive number of bladder-worms infests the bodies of swine, they become, according to Zürn,[1] dull and melancholic. They no longer curl their tails, but show pale proboscides and colourless mucous membrane in the mouth. They cease to take their food, so that marked emaciation sets in. The mouth has a bad smell, and on the neck, head, and shoulders œdematous swellings appear. The bristles fall off still more readily, and exhibit usually, as Aristotle observed, bloody lower ends. The weakness increases greatly, and leads to a paralysis of one or other of the extremities, and usually to a distinct paraplegia. The emaciation gradually increases, and the grunt becomes almost a croak. Then diarrhœa sets in, which increases the stink, and this continues usually till the death of the animal puts an end to its sufferings. When the bladder-worms occur in the brain, then one observes, in addition, cramp, madness, or paralysis.

When the disease is but slight, then the flesh is normal in appearance, apart from the presence of the embedded worms, but in extreme cases, and especially in fatal ones, the flesh appears pale and discoloured, and infiltrated with serum, which flows out in little streams when putrefaction begins.

These complex symptoms of bladder-worm disease cannot be likened to the acute Cestode tuberculosis, which we saw in the ox after infection with *Tænia saginata*, either in respect of symptoms or of efficient factors. The latter consists essentially in the reaction of the organism against the imported Cestode brood, while the bladder-worm disease is rather the consequence of the pressure exerted by the parasites on their surroundings. The phenomena of acute Cestode tuberculosis do not occur in the pig even after abundant introduction of germs. Gerlach, indeed, reports the case of two young pigs which died after a lapse in the one case of nine, and in the other of twenty days, after feeding with *T. solium*, and that with more or less distinct symptoms of intestinal inflammation, and is therefore inclined to suppose that an abundant importation of tape-worm eggs may be fatal,

[1] "Schmarotzer der Haussäugethiere," Bd. i., p. 137.

through inflammation being set up in the wall of the intestine and in other organs.[1] There is, however, no proof of the correctness of this supposed connection of cause and effect. Other investigators have always succeeded in keeping their animals alive, and free from any pathological symptoms, when fed repeatedly with long chains of proglottides, even though they experimented with young pigs, which, according to Gerlach (p. 495), are alone suited for the development of the bladder-worms. The fact that the young bladder-worms lie at first almost free, and only gradually form a firm capsule, while those in the ox have from the first a thick sheath of exuded lymph, is certainly not in favour of the idea that the pig reacts against the invading brood as strongly as does the ox. We need hardly note that this is very important, for the pig, from its mode of life, is much more frequently infected than the ox.

The genetic relation between the bladder-worm and *Tænia solium* makes it evident that its occurrence and frequency in various districts must be very varied. But it is not the distribution and frequency of the tape-worm which alone determine this, for it depends still more, perhaps, on the condition and housing of the swine. Where the swine are bred in a half-wild state, being generally driven out to the meadows or the oak-woods, where they have to seek their own food, then their opportunities of infection are more frequent than when they are kept and fed in the styes. In fact, the introduction of the custom of feeding in the stye has in many cases markedly reduced the frequency of Cysticercoid disease. This can of course be hoped for only when the pigs are kept in a cleanly way, and not allowed to get near dung-heaps or privies, which are always to a certain extent dangerous. Their food must of course be freed from all possible contact with human excrement. Particularly must any tape-worm patient be removed as rapidly as possible from near the swine, since his presence is a source of danger to the whole herd. This is strikingly illustrated by an observation made by Fürstenberg,[2] which tells us of a tape-worm patient who once infected a whole herd of fifteen pigs, which had broken through the barrier separating them from the privy. Two of the number exhibited an acute affection, which was designated Cestode tuberculosis with doubtful accuracy, and the others were rendered quite useless.

Since human excrement is deposited in very varied places whereever man exists, it is readily conceivable that wild swine may also be occasionally infected, but this is rare, as one would expect in the case of animals living far from the dwellings of man.

[1] *Loc. cit.*, p. 68.

[2] Mosler, *Archiv f. pathol. Anat.*, Bd. xxiii., p. 426, 1862.

It is quite different, however, in the case of the Indian swine, as we have learned from English physicians stationed in the Punjab. The half-wild animals round the villages are specially fond of frequenting the public dung-heaps, to which we have already referred in connection with the bladder-worms of the ox (p. 473). Day after day, according to Flemming,[1] they may be seen on the look-out, waiting till the natives finish operations. They hardly give them time to do so, and have sometimes to be driven off by force. Since *Tænia solium* is hardly less common in India than *T. saginata*, it is readily seen that the bladder-worms of the pig must also be excessively common.

Similar circumstances give rise to similar consequences. Thus we understand why in Ireland, Slavonia, and certain parts of North America, the bladder-worms of the pig are of the commonest occurrence.

In Germany, too, and in Central Europe, there are localities where the swine are so frequently and so abundantly infected with bladder-worms that they have quite a bad reputation with dealers and butchers.[2] These are mostly country districts, where the excrement of the inhabitants is carelessly deposited, and is easily accessible to the swine. Villages furnish a larger contingent of measly swine than do towns, though the latter afford more instances of tape-worm patients, owing to the greater consumption of flesh, or rather owing to the immense number of animals imported from the country for town consumption.

Although these facts are generally known, we have but few satisfactory data as to the occurrence of bladder-worms,—much fewer than in the case of *Trichina*. The former, though occurring more abundantly, have less hygienic importance, since, from their demonstrable size, they involve less danger than do the others, which have a rarer and more hidden occurrence.

Out of 1,728,600 swine examined in 1876 in Prussia, there were, according to the newspaper reports, 4706 infected with bladder-worm, *i.e.*, 1 for every 370. Similarly, in Vienna[3] there were in about 10,000 swine 163 infected (1·307), in the Cassel district,[4] out of 149,500 examined in 1872-74, there were only 158 "measly," or 1·945. This last ratio can hardly be directly compared with the former, since the less serious cases were probably unnoticed. Within a certain range one finds marked divergences, as may be best seen perhaps

[1] Cobbold, "Parasiti interni, &c.," p. 46.

[2] Thus von Siebold notes in his "Band- und Blasenwürmer" (p. 114) that the swine imported into Neufchatel from the surrounding country are almost all "measly," while such a disease is almost unknown in the west of Switzerland.

[3] *Oesterr. Monatschr. f. Thierheilk.*, No. 2, p. 14, 1876.

[4] *Vierteljahrsschrift f. gerichtl. Medicin*, Bd. xxv., p. 202.

from a communication of Mosler's,[1] according to which there were in 20,000 swine only 9 markedly infested with bladder-worms (1 : 2222), although every eighth animal harboured a few *Cysticerci.* It is, indeed, possible that the bladder-worms which were abundantly found in the omentum and viscera did not exclusively belong to *Cysticercus cellulosæ,* but I think, from the results of my experience in Giessen in the year 1860, that we may conclude that there are districts in Germany in which 2·3 per cent. of the swine are infected with bladder-worms in varying numbers.

Reports from Italy tell the same story. Pellizzari estimates the number of specially measly swine at 3-4 among 11,000-12,000 (one for every 3000-4000), while Perroncito[2] reports that, according to the statement of an official inspector (Langueyeurs), one diseased specimen for every 250 occurs in Turin, while in Milan (according to a calculation based upon three months) 80 were found in 5500, or one in seventy.

However imperfect these statistical results may be, this much is certain, that *Cysticercus cellulosæ* in the pig is by no means rare, and, indeed, is far more abundant than *Trichina.*[3]

This is not only true in regard to the pig, but also, as we have recently learned from the computations of Müller[4] and Dressel,[5] for man. The various results are conflicting, even those of the same authors varying when they have observed in different localities, so that we are perhaps justified in believing that the occurrence of the *Cysticercus* is as much determined by local conditions as is the occurrence of the *Tænia;* at all events the reports seem to agree in establishing a diminution in the frequency of the bladder-worm.

If one calculate from the existing data as contributed by the Pathological Institutes of Berlin (Virchow), Göttingen (Förster), Dresden (Zenker), and Erlangen (Zenker), one finds in a total of 9753 *post-mortem* examinations 127 cases of *Cysticercus cellulosæ,* or 1·3 per cent. One bladder-worm subject occurs in about seventy-six examinations, a ratio which is more than double that similarly computed for *T. solium* (p. 531). It is, however, open to question whether we can directly compare these two cases, and conclude that *Cysticercus cellulosæ* is twice as frequent as *T. solium.* For the results of these examinations do not give one any correct impression as to the numerical frequency of parasites, especially as regards those which occur incidentally, and do not directly call for medical assistance. In numerous cases of *Cysticercus* the trouble is a very serious one, sometimes occasioning death; but, besides these, there are a

[1] *Loc cit.*, p. 426. [2] *Loc cit.*, p. 64. [3] See Vol. II.
[4] "Statistik der menschlichen Entozoen." Dissert. inaug., Erlangen, 1874.
[5] "Zur Statistik des Cysticercus cellulosæ." Dissert. inaug., Berlin, 1877.

great number of more trivial cases which never call for clinical treatment.

The highest ratio furnished by our existing data is that of Berlin, where the *Cysticercus* during the years 1866-1875 occurred, according to Dressel, not less than eighty-seven times in 5300 dissections—that is, 1·6 per cent. In 1866 Virchow estimated this per-centage at two,[1] and with this agrees Rudolphi's report that in the anatomical threatre at Berlin the *Cysticercus* only occurred four or five times in about 250 bodies. In Dresden the state of the case is very similar. Between 1852 and 1862 twenty-two cases of bladder-worm occurred out of 2002 examinations, that is, 1·9 per cent.; while in the Pathological Institute at Erlangen fourteen cases occurred among 1812 bodies, *i.e.*, 0·78 per cent. (Müller). In Göttingen the per-centage was 0·63, or four out of 639. In Würzburg during seven years Virchow only saw *Cysticerci* on very rare occasions, while the famous helminthologist Bremser in Vienna had never seen one at all. The occurrence of this parasite was first established there in the course of pathological investigations,[2] but the cases were so few that they cannot at all be compared with those occurring in Berlin, and in other districts of North Germany.[3]

The age and sex of the bladder-worm patients have been recorded only by Dressel. From his report we first note the fact that the majority of patients (thirty-nine out of the seventy-four whose age was noted) were in the prime of life—a result which also holds good in regard to the adult *Tænia*. Six of them were above seventy, one was eighty-four years of age. In children the *Cysticercus* was only twice found, once in a child three years old, and again in one "who seemed to be only a few days" old.

The bladder-worms in adults were often calcified, so that one was perhaps justified in referring them to an introduction in earlier years, but, on the other hand, there were also some instances of fresh *Cysticerci*. The latter prove at least this much, that the introduction and development of the tape-worm brood is in the case of man in no-way restricted to a definite age, as it seems to be, according to Gerlach,

[1] V. Graefe, *Archiv f. Ophthalmologie*, Bd. xii., p. 2.

[2] Rokitansky, "Pathol. Anat.," Bd. ii., *div. loc.*

[3] In agreement with this is the fact that Hebra observed among 10,000 patients suffering from diseases of the skin only one case of bladder-worms in the subcutaneous tissue, and that the Viennese oculists sought vainly for bladder-worms in the eye, while those in Berlin noticed hundreds. Mauthner reports that in 30,000 eye-patients he had never seen a *Cysticercus*. Berlin, in Stuttgart, found one among 40,000 patients, and Wecker, in Paris, one in 60,000; while v. Graefe, in Berlin, estimates its occurrence at one per thousand, and A. Gräfe and Hirschberg at a still greater per-centage. (See Græfe and Saemisch, "Handb. d. ges. Augenheilk.," Bd. iv., v., vi., *loc. div.*). Bladder-worms in the eye are rare in Switzerland and in England.

in the case of the pig (p. 495). If the same conditions held good in regard to man, then the maximum occurrence would be reached at the end of childhood and not after maturity.

Especially striking and surprising is the above-mentioned case of *Cysticercus* in a child "some days old." It is so well worth attention, that one cannot but lament the brevity with which it is mentioned. Since the bladder-worms are hardly recognisable as such "some days" after their introduction, but require, as we have seen, two months for their development, the infection must surely have taken place during fœtal life.[1] It is possible that the mother was infected, and that from this source the fœtus was penetrated by the wandering brood. The six-hooked embryos might easily pass in some way or other (by the blood-vessels ?) to the young, and would there gradually become *Cysticerci* either in the muscles or in other organs.

The process which we here suppose is not perfectly isolated, since we know of other Helminths, which, during their internal wanderings, pass from the maternal body into the embryo (p. 67, note); but after all the entirely negative results which we have in this connection in regard to *Trichina*,[2] we were but little prepared to find this phenomenon exhibited in the case of *Cysticerci*.

It is a surprising fact that the majority of patients suffering from bladder-worms are males, while *T. solium* is much more frequent in women. There is no doubt as to the fact, which is evidenced not only by Dressel's tables, but also by Küchenmeister's reports on *Cysticerci*[3] in the brain, and by the observations of v. Graefe on the occurrence of bladder-worms in the eye.[4] Of the 87 cases noted by Dressel, 53 were males (2·4 per cent.) and only 34 females (1·6 per cent.). Küchenmeister found that among men *Cysticerci* in the brain were almost half as numerous again as among women, while v. Graefe reports that almost two-thirds of the 80 cases of bladder-worm in the eye belonged to the male sex.

This constant preponderance of the male sex shows, of course, that infection with embryos of *Tænia* is favoured by the habits and customs of men. It may be suggested at least that women are more orderly and on the whole more cleanly than men.

[1] We do not know the meaning of "some days," but it is possible that the infection took place during birth; that the child in passing through the vagina might, along with the secretion, swallow some proglottides or eggs issuing from a *Tænia* living in the intestine of the mother. The eggs have, according to Lewin, been found by Hausmann in the mouth of the child.

[2] See Vol. II.

[3] "Ueber die Cysticercen des Hirns und ihr Verhältniss zu Lähmungen, Epilepsie und Geisteskrankheiten," *Oesterr. Zeitschr. f. pract. Heilk.*, 1868.

[4] "Bemerkungen über Cysticercus," *Archiv f. Ophthalmologie, loc. cit.*

The above fact leads us to the question—By what ways and means does man become infected by these embryos? Of course an infection of some sort must precede the appearance of *Cysticerci*. The days in which one believed in a direct transmission of bladder-worms from "measly" flesh are so long past, that it seems incredible when we read, *e.g.*, that even in 1851 Küchenmeister regarded not only those who reared and killed swine, &c., but also those working with raw leather and skin, as peculiarly liable to bladder-worm disease.[1]

The most direct and most frequent source of infection is, of course, in the eggs, which are dispersed round about the abode of the tape-worm, and are also widely distributed in the open air with the excrement. Invisible to the naked eye, they may easily pass more or less directly into man. Sometimes in drinking water or in vegetarian diet, sometimes in food into which the embryos have accidentally found their way, or by the hand, to which they have adhered. A dirty, untidy, crowded house increases the risk of infection enormously, and hence the frequency of the disease is (according to Stein) much greater among the lower classes.

Where the infection is due to isolated eggs, the resulting bladder-worms occur either singly or in small numbers. But this is not always the case. On the whole, the numbers found in man are much smaller than in the pig. And lately the results of v. Graefe and Dressel have shown that cases of solitary occurrence are very frequent.[2] But there are also cases known in which the bladder-worms were as numerous as in the abundantly infected swine. Thus Stich dissected a woman, a turf carrier, in whose muscles and subcutaneous tissue between 400 and 500 bladder-worms at least could be counted. Lanceraux reports also the case of a rag-picker,[3] whose muscles, especially in the thorax, were so abundantly penetrated by bladder-worms, that their number was estimated at over 1000. Similarly Lessing[4] reports the presence of more than 1000 *Cysticerci* in the body of an insane patient. In Bonhomme[5] we read of a patient seventy-seven years old, who, besides 900 bladder-worms in the muscles, bore also upwards of 2000 in the subcutaneous tissue, besides numerous specimens in the brain and lungs. A policeman, thirty-two years old, who died with severe symptoms of cerebral disease, exhibited on dissection numerous *Cysticerci* in the brain, and also a great number of muscle bladder-worms, especially in the ex-

[1] *Archiv f. pathol. Anat.*, Bd. iv., p. 65, 1851.

[2] Dressel's reports yield the surprising result that in almost 37 per cent. there was but one *Cysticercus*.

[3] *Archiv. génér. méd.*, t. xx., p. 545, 1872.

[4] *Schmidt's Jahrbücher*, Bd. xcix., p. 98, 1858.

[5] *Comptes rendus soc. biol.*, t. v., p. 62, 1864, or *Archiv. génér. méd.*, t. i., p. 355, 1865.

tremities, which seemed almost "stuffed" with them.[1] Similarly Gubain reports[2] a case where the muscles and internal organs (heart, brain, and viscera) were so full of bladder-worms "that had one not seen the resulting disorganization one would not have believed it."

Such occurrences cannot, of course, be referred to the introduction of isolated eggs; it must have taken place *en masse*, either by a large number of newly expelled eggs,[3] or of eggs still within the proglottis. In other words, whole proglottides or series of them may be transferred to the stomach of their host, and there liberate the eggs.

We can hardly bring ourselves to suppose that it can ever happen that man should infect himself with a whole brood as the swine do. One must, however, face the facts, apart from any æsthetic prejudice, and there are several disgusting possibilities of this sort.

First, we must remember that there are among men coprophagous persons even besides the insane, and such an one may easily become infected like a pig.[4] The only question is as to the real existence of such a habit. On this point we have suspicion rather than fact to go upon. But at any rate this does not exhaust the possibilities of infection *en masse*, for the proglottides may also by themselves find their way to the mouth.

We cannot suppose that any one would wittingly swallow a tape-worm joint. But apart from the possibilities open to children and the insane, the tape-worm patient may readily infect himself with the proglottides during sleep by lifting the hand to the mouth. The transference is, however, more frequent when, by shrivelling and drying up, the proglottides become indistinguishable, are then carried by chance in various directions, which distribution sometimes not unnaturally results in their being swallowed. Disorder and uncleanliness in the room and house are fertile sources of increased risk.

When an inmate of the house or a member of the family suffers from *Tænia solium*, there is obviously special necessity for cleanliness and care. The linen of the patient should be frequently changed, the buttocks and hands should be frequently washed, the excrement carefully removed, and the voided proglottides destroyed, if possible, by burning, without touching the hands. The patient is himself in greatest danger of self-infection.

[1] Onymus, *Gaz. des hôp.*, p. 237, 1865.

[2] Quoted by Stich, *loc. cit.*, p. 176.

[3] We may also note that even after an abundant introduction, only one bladder-worm, or but a few, may develop.

[4] In fact Wendt and Birch-Hirschfeld have found numerous *Cysticerci* in the brain of a coprophagous tape-worm patient. Wendt, *Allgem. Zeitschr. f. Psychiatrie*, Bd. iii., 1872; and Birch-Hirschfeld, *Jahrb. d. pathol. Anat.*, p. 203, 1876.

This latter does, indeed, occur very abundantly among bladder-worm patients. Küchenmeister is even of the opinion that the above-mentioned preponderance of male patients is due to greater possibility of self-infection. In support of his position he refers[1] to the male clothing, which makes the removal of spontaneously liberated proglottides difficult, and also to outdoor work, which frequently compels a man to ease himself in the open air under circumstances which make defiling of the hands very easy.

On the other hand, there are investigators, and among them such a prominent scholar as Virchow, who would refer but few cases to self-infection, and are even inclined to question its existence. They refer to the results of statistics, according to which the occurrence of a *Tænia solium* has been but seldom proved in a bladder-worm patient, so that the cases of their associated occurrence are probably accidental, and do not admit of any conclusion being drawn as to the origin of the *Cysticerci.*

Graefe is their chief witness, who,[2] out of eighty cases of *Cysticercus,* found only five or six in which he could prove the presence of a *Tænia,* while in a great number of cases the persons who shared the same room with the patient suffered from tape-worm. Dressel's testimony is still more emphatic; for in the cases compiled by him from clinical reports, there was not one of a tape-worm and bladder-worm co-existent, though he acknowledges that, not knowing the history of the patients in question, he could not say that the patients had not formerly suffered from tape-worm. But this last question is a most decisive one; for while the bladder-worms persist after they have once been developed, the tape-worm often lives for a comparatively short time in the intestine of its host.

For this reason we may assume that cases of co-existence of tape-worm and bladder-worm represent but a small fraction of those cases in which the bladder-worm hosts have been also tape-worm hosts. The twenty to twenty-one cases of such co-existence, which Lewin[3] has earned our thanks by collecting from the scattered and hardly accessible reports, are by no means of such little weight as one might at first sight suppose. And this, too, must be remembered, that they all refer to recent decades, at a time when the relations between

[1] *Loc. cit.*, second edition, p. 108. [2] *Loc. cit.*

[3] *Loc. cit.*, p. 651. Küchenmeister erroneously reports the number only at eleven. Two other cases have been since discovered by Müller, a third by Heller (Ziemssen's "Handbuch," Bd. iii., p. 331; Eng. transl., p. 599), and a fourth by v. Wecker (v. Graefe u. Sämisch, "Handbuch d. ges. Augenheilkunde," Bd. iv., p. 713). Boyron ("Etude sur la ladrerie chez l'homme," Paris, 1876) also reports cases of two bladder-worm patients also infected with tape-worm (Observ. i. and iv.), so that the total number of cases is about twenty-seven.

Cysticercus cellulosæ and *Tænia solium* were as yet unapprehended, and when the presence of tape-worm in cases of bladder-worm might attract no special attention.

It is, however, by no means necessary that the transmission of a brood should take place through the mouth. The eggs are, indeed, in all cases subject to the action of the gastric juice (p. 153), but a transference from the intestine into the stomach may take place directly when the contents of the former are driven forwards by antiperistaltic contraction. Sometimes it is but single proglottides which pass back in this way, sometimes longer stretches of joints, so that an infection may thus be brought about, resulting in an abundant occurrence of *Cysticerci*. Such being the case, it is quite possible that one or other of the above-mentioned cases was due to a self-infection of this sort.

The fact that there are numerous cases of tape-worms (*Tænia solium* of course) where the host never becomes infected by bladder-worms, cannot, of course, be used as an argument against the assumption of this "entocœlic" self-infection. It could be used as such only if the digestion of the egg membranes and the liberation of the embryos were possible while the eggs were still in the intestine. This is, indeed, alleged by Küchenmeister,[1] and more recently by Klebs[2] and Lewin. In this case, the existence of a tape-worm host without bladder-worms would be exceptional, while we know that exactly the reverse is true.

In rare cases the transference of proglottides into the stomach may be facilitated by the abnormal position of the tape-worm. Sometimes one finds the worm hanging upwards[3] in the intestine, so that the proglottides are approximated to the stomach. It is doubtful, however, whether this position was permanent. At any rate, one must remember that the position of the tape-worm in the intestine is determined by extraneous forces (pressure of the chyme, contraction of the intestine, &c.), as well as by the motions of the worm itself.

The proglottides passing into the stomach from the intestine can cause infection only when they remain some considerable time in the former. When they merely pass into the stomach to be

[1] "Parasiten," first edition, p. 12. Küchenmeister maintains that the embryos may be liberated, and may develop even in the œsophagus. Only after I published my objections ("Blasenbandwürmer," p. 102), and proved experimentally that the embryos could only be liberated by the action of the gastric juice ("Parasiten," first edition, p. 116), did he change his opinion. That did not, however, hinder him from asserting in pp. 98 and 115 of the new edition that he was the first to show that a transference into the stomach was necessary for the liberation of the embryos. We do not need now-a-days seriously to contradict or disprove the statement of Küchenmeister, that the bladder-worms found in the peripheral regions, such as the conjunctiva, arise from direct immigration from outside.

[2] "Handbuch d. pathol. Anat.," p. 301, 1868.

[3] A case of this sort (by Siebert) is found in da Conta, *loc. cit.*, p. 162.

expelled by the mouth, the action of the digestive juices has not time to liberate the embryos. Thus we understand that among the cases enumerated by Lewin,[1] in which larger or smaller pieces of *Tænia solium* were voided, there are only two instances (those of Kuntzmann and Witthauer) in which bladder-worm disease has been certainly established. On the other hand, Dressel cites a case in which a tape-worm (it is not expressly said that it was *T. solium*) was found in the duodenum and stomach, "in a place which could hardly have been more favourable for self-infection," but yet none took place. It is impossible to prove, however, that the worm occupied this unusual position during the life of the host, and did not assume it on the approach of death.

But, granted that the infection has taken place in some way or other, then the embryos distribute themselves in the body according to circumstances, and become bladder-worms. How they wander we cannot say with certainty. At any rate, they may reach any part or organ of the body, except, perhaps, the bones,[2] which are probably protected more by their being ill-suited for development than by their inaccessibility. The bladder-worms are found, strangely enough, but rarely in the liver—a contrast to the *Echinococcus*.

From the analogy of its occurrence in swine, we are led to the conclusion that it is the muscles, or rather the intra-muscular connective-tissue, which the bladder-worms most frequently inhabit. The results of dissections seemed in harmony with this till our attention was lately directed, especially by Dressel's reports, to the extraordinary frequency with which this worm occurs in the brain. Whether this result of pathological examination is a true expression of the real state of the case is, however, doubtful, since bladder-worms in the muscles are apt to escape the notice of pathological anatomists and of clinical surgeons, while the cases of bladder-worms in the brain as naturally demand their attention. The deceptiveness of statistics obtained from purely pathological examinations is most strikingly shown by the fact that Dressel notes in his eighty-seven cases only three instances of bladder-worms in the skin, while Lewin observed as many within a single year. The frequency of the bladder-worms in the eye has been demonstrated by means of the ophthalmoscope; but before this instrument was used they were held as great rarities. In pathological anatomical institutes they are even yet so rare that neither Müller nor Dressel mentions them. The thirty-six cases of the former refer for the most part only to the brain (twenty-one), the

[1] *Loc. cit.*, p. 658.

[2] It is doubtful whether the case in Froriep's "Chirurg. Kupfertafeln" (438) is established or not.

muscles (twelve), and the heart (three); and the reports are so unequally divided between Dresden and Erlangen that, *e.g.*, out of twenty-two cases, eleven cases of *Cysticerci* in the muscles are recorded in the former, while, out of fourteen cases in Erlangen, only a single one is reported.

According to Dressel's lists, among the eighty-seven cases of bladder-worms at Berlin, seventy-two were in the brain, thirteen in the muscles, and six in the heart. There were, besides, three cases of *Cysticerci* in the lungs, three in the subcutaneous tissue, and two in the liver. These cases enumerated exceed the total eighty-seven; but this results from the fact that the bladder-worms are by no means always restricted to a single organ. This is generally the case, however, when they were found in the brain or eye; for, among the seventy-two cases of cerebral bladder-worms, there were no fewer than sixty-six in which the parasites were restricted to these organs. Similarly Graefe reports that in the eighty cases of bladder-worms in the eye observed by him up to 1866, there were no patients in whom he could demonstrate their presence elsewhere, except two, who possibly harboured them in the brain.[1] When the bladder-worms occur in other organs, then the local limitation seems to be less frequent, as may be inferred from the fact that in Dressel's cases there were but four in which the bladder-worms occurred only in the muscles, and only two in which they were confined to the heart.

The *Cysticerci* in the brain are usually found in the membranes and in the cortex. The Sylvian fissure is specially frequented, as are also the large ganglia, the corpora striata, and the optic thalami. The fourth ventricle occasionally contains them, as also the choroid plexus. On the contrary, bladder-worms have been found only four times in the substance of the cerebrum and cerebellum.[2] They occurred still more rarely at the base of the brain. On the frontal lobes they were found four times, on the lower surface of the pons once, and also once between the two optic nerves. As to the *Cysticerci* in the muscles, no favourite place could be inferred from Dressel's cases, although it certainly seemed as though the pectoral muscles are very frequently diseased. But there was hardly a group of muscles which was avoided by the bladder-worms; the muscles of the extremities were as much infected as the intercostals, or those of the abdomen and the

[1] Dr. R. Schulz of Brunswick told me of a case of *Cysticercus* in the retina which occurred along with many in the subcutaneous tissue.

[2] This may be inferred from Küchenmeister's report (*Oesterr. Zeitschr. f. pract. Heilk.*, 1866). In the eighty-eight cases here collected the bladder-worms were found forty-nine times in the membranes, thirty-nine times on the surface of the hemispheres, thirty-six times in the great ganglia, but only nineteen times in the central substance, and eighteen times in the ventricles.

psoas. The musculature of the ventricles and auricles was frequented, as was also the inner layer of the pericardium and endocardium. Under the superficial membrane, the bladder-worms not unfrequently form vesicular dilatations, and (especially in the endocardium) papillar or stalked appendages; and a *Cysticercus* has been observed even in the walls of the blood-vessels.

Of special interest is the occurrence of *Cysticerci* in the eye, partly because it is common and soon makes itself perceptible, partly also because it affords opportunity for observing the worm in its natural environment, and of following out its development. We owe this to the discovery and application of the ophthalmoscope, and the sensation which its revelations excited was all the greater since previous experience of bladder-worms in the eye had been limited to but few cases.[1]

Von Graefe, to whom we owe our first account of these surprising discoveries, calculates, on the strength of a very large mass of statistics,[2] that the occurrence of the *Cysticercus* in the deeper parts of the eye at about one per thousand among the patients at the Berlin Ophthalmic Institute. In the anterior parts of the eye he only reports nine cases (five in the conjunctiva, two in the anterior chamber, one in the lens, and only one in the orbit); but these represent hardly the eighth part of those found in the vitreous humour, or in the subretinal tissue. Those in the latter situation are by far the most frequent, standing to those found in the vitreous humour in the ratio of 2 : 1.

In the cases mentioned by v. Graefe it was always only a single *Cysticercus* which inhabited the eye; and so also with others, with the exception of a single case observed by O. Becker, where one *Cysticercus* occurred in the vitreous humour and another in the retina. This solitary mode of occurrence is peculiar to man, for in the pig the eye occasionally contains a considerable number. Nordmann counted in one case twelve, of which six were in the vitreous humour, and the other six between the sclerotic and the choroid.[3]

In the chambers of the eye the *Cysticercus* is almost always free—*i.e.*, without a capsule, and swimming in the fluid; so that its position may vary with the attitude of the head and the direction of the eyes, as well as with its own movements, which consist partly of an undulating peristalsis of the bladder, but principally of an alternate protrusion and retraction of the head. At the point of insertion of

[1] The first observation on the occurrence of a bladder-worm in the eye (the anterior chamber) is furnished by Schott and Sömmering.—Oken's *Isis*, p. 717, 1830.

[2] From the *Verhandl. Berlin. Med. Gesellsch.*, 1867-68, p. 96, 1871, I extract the statement that v. Graefe has observed over 100 cases of bladder-worms in the eye. The observations in the text rest on v. Graefe's notes on *Cysticercus* (*Archiv f. ophthalmologie*, Bd. xii., p. 174).

[3] *Mikrographische Beiträge*, Th. i., p. 13 : Berlin, 1832.

the process one observes a blunt, proboscis-like projection.[1] In the interior of this the quadrangular head may be recognised, which is usually soon extruded, so that the whole appendage, with narrow neck and wrinkled body, is free down to the constricted base. Generally the movement of the rostellum and suckers is to be seen; they are protruded in varying fashion, the head rotates on the neck, and the whole appendage exhibits a periodic retraction, so that it sometimes approaches the bladder, and at other times projects directly from it. At certain times the movements are almost continuous, while at other times the appendage hangs out almost immoveably from the bladder, so that one might readily suppose the worm to be dead.[2] The movements of the worm are usually excited by the contraction of the iris; by the use of atropine there is a marked diminution, but whether by direct or indirect operation is uncertain. The diamond-like glitter which one sometimes sees when the rostellum is protruded depends probably on the hooks, which change their position somewhat in consequence of the movement. Similarly, the point-like excrescences on the bladder can hardly be anything but the above-described microscopic projections characteristic of the *Cysticercus cellulosæ.*

As in the aqueous, so it is in the vitreous humour, only of course with this difference, that the movements are more and more restricted by the threads and membranous thickenings which gradually develop. In many cases a sort of capsule is formed round the worm.

In the first edition of this work I have already expressed the supposition,[3] which has been reiterated by my old friend v. Zehender, that the bladder-worms of the chambers of the eye and of the vitreous humour were not developed there, but were first embedded in the adjacent membranes—iris or choroid—and that they subsequently became free, just as I have proved in regard to the bladder-worms of the body-cavity (*C. pisiformis* and *C. tenuicollis*), which, after their passage from the liver, remain for a while free before they are ultimately surrounded by a cyst.

On closer scrutiny of the ophthalmological literature on this point, and especially of the account which v. Wecker and Leber have given in the well-known text-book on general ophthalmology by v.

[1] See von Wecker in "Handbuch d. ges. Augenheilk.," by von Graefe and Sämisch, Bd. iv., p. 708.

[2] See the observations of Sömmering (*loc. cit.*), and of Mackenzie, *Med.-Chirurg. Trans.*, vol. xxxii., 1849.

[3] Küchenmeister expresses the same supposition in the second edition of his work on parasites (p. 250), and imagines that he renders his own opinions of greater weight by calling mine "an anatomical presentiment."

Graefe and Sämisch on the diseases of the vitreous humour[1] and retina,[2] I am convinced that my opinion was perfectly justified. What is here given us is little less than a complete history of the bladder-worms inhabiting the vitreous humour, and an adequate demonstration is given of the fact that these worms originate in the subretinal membranes.

In ophthalmoscopic examination the bladder-worm appears first as a bluish-white, sharply defined body, and lies behind the retina, so that the vessels of the latter extend over it. The bladder is easily flattened by pressure, and exhibits the head as a clear spot shining through. The latter is always invaginated, and never protrudes, although the wall of the bladder constricts and dilates in an undulating fashion. In many cases the worm moves away from its original seat, loosening and disturbing the retina over an increasing area. The vitreous humour is also penetrated by delicate membranous opacities, which extend in front of the bladder like a veil or curtain, with dark folds and stripes. Subsequently the retina is partially destroyed by the increasing pressure of the bladder, so that the latter falls forward into the vitreous humour. Sometimes one sees how the neck with the head is protruded through the opening. When the whole worm has broken through into the vitreous humour, its former seat may still be seen as a discoloured spot of irregular form, while the point of rupture can be but rarely seen with any distinctness, owing to the turbidity of the vitreous humour.

If frequent change of position, or copious discharge of fluid under the retina, have led to an extensive or total loosening of the same, the *Cysticercus* remains lying where it was, and does not break through into the vitreous humour. The bladder then becomes encapsuled by connective tissue, which gradually acquires a firmer nature, and may finally undergo a partial ossification.

FIG. 298.—Subretinal *Cysticercus* in the eye, after v. Wecker (nat. size).

On sections of such eyes the bladder is seen lying between the choroid and the retina. Round about the worm, or over the whole extent, the retina is much thickened by proliferated connective tissue, and has fused with the capsule, or is sometimes atrophied. Similarly the choroid is sometimes also involved in the exuberant growth of connective tissue.

Less frequently there is formed round the parasite, at an early stage, an envelope of delicate vascular connective tissue, which raises

[1] Bd. iv., p. 709.

[2] Bd. v., p. 708.

the still transparent retina like a tumour, but is sometimes deserted by its inmate, which then settles at another place, and is encapsuled anew.

The observations here related do not exclude the possibility that, besides the bladder-worms which subsequently pass into the vitreous humour, there are also some which have developed there from the first. But while no positive argument can be given in favour of this idea, on the other hand, all we know of the development of *Cysticercus* leads to the supposition that the first stages must always be spent in a vascular tissue. We are, however, justified in believing that the exit of the bladder-worm from the surrounding tissue might sometimes take place at an earlier stage of development, at a time when the changes in the retina had not yet attained their subsequent extent, and were therefore less noticeable. But the incipient stages of the Cysticercoid disease in the eye have as yet eluded investigation.[1]

In the bladder-worms inhabiting the anterior chamber of the eye, an early exit is perhaps more frequent than among those infesting the vitreous humour, as one could, indeed, infer from the fact that the aqueous humour presents much less resistance to the growing bladder-worm. Indeed, the *Cysticerci* are usually found free in the aqueous humour. Yet there are cases which demonstrate a connection between these free forms and the iris; an actual union has, indeed, been repeatedly observed.[2] Thus Dalrymple observed a case where the bladder was so fastened to the iris that the latter looked as though perforated by it. In another case (recorded by Teale), the worm connected by its cyst with the iris was hardly bigger than a hemp-seed, and from the shortness of the neck might be seen to be quite a young *Cysticercus*. The case lately described by Küchenmeister[3] ought also to be noted; for here, besides the free *Cysticercus* in the anterior chamber, there was also a connective tissue cyst adherent to the posterior wall of the iris, which latter was reasonably regarded as its bladder. Since it contained only a clear fluid, it must have closed up after the exit of its inmate and become filled with serum.

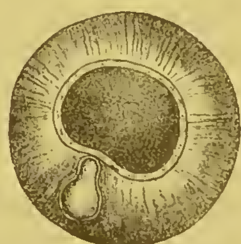


FIG. 299.—Bladder-worm in the anterior chamber of the eye, after v. Wecker. (× 3.)

The bladder-worms of the interior of the eye are not the only ones found free within serous cavities. In the ventricles of the brain they

[1] The smallest bladder-worms seen by v. Graefe measured 3 to 4 mm. In three or four weeks after the appearance of the first, he noticed, with the ophthalmoscope, marked changes. Some weeks later, the worms had a diameter of 5 to 6 mm., and after two years they had increased to 11 mm. *Archiv f. Ophthalmologie*, Bd. xii., 2, p. 188.

[2] See v. Wecker, "Handbuch d. ges. Augenheilkunde," Bd. iv., p. 575.

[3] "Parasiten," second edition, p. 249.

sometimes occur, usually without any envelope. We need not again note that here also we have to do with a secondary condition.[1] The worms in question obviously originate in the choroid plexus, which is sometimes, as we have seen, inhabited by bladder-worms.

The same may be said of the bladder-worms which are found in the meshes of the arachnoid and pia mater on the surface of the brain. They have usually an irregular form, and sometimes vary so much from the ordinary type that their true nature is not evident at the first glance. These extreme cases are called "branched" *Cysticerci* (*C. racemosus*) by Zenker, who lately directed our attention to them.[2] The name is not inapt, since they often appear as long extended cylindrical bodies (sometimes 8, or even, according to Heller, 25 cm. long), of varying thickness, and giving off in their course numerous more or less large bladders. The latter are not unfrequently stalked, and are beset with irregular daughter-bladders, so that their appearance varies greatly. Heads are but seldom found, and at most only one to each bunch. They have the characters of *Tænia solium*, and show their connection with it by sometimes occurring along with the genuine *Cysticercus cellulosæ* (as in Marchand's case), and by the latter being connected with them by intermediate stages.[3] Besides, they have also the microscopic protuberances of the cuticle, and the scattered calcareous bodies like the common *Cysticercus cellulosæ*.

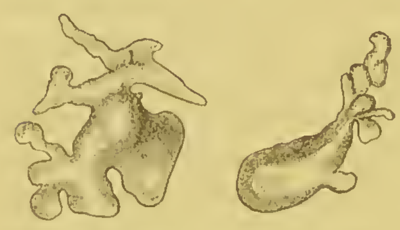


FIG. 300.—*Cysticercus racemosus*, after Marchand (nat. size).

We do not yet know by what circumstances this unusual growth is determined, but we may conjecture that the form of the enclosing space and the course of the blood-vessels which penetrate the membranes of the brain and pass out on to the surface, have something to do with it. This fact also ought to be noted, that, according to Marchand, the attached bladders do not merely arise by protrusion of the wall of the bladder, but result in part from buds which are formed on

[1] In the case observed by Zenker, in which a *Cysticercus* was found free in an aneurismal sac attached to the vertebral artery (Heller, in "Ziemssen's Handbuch," Bd. iii., p. 344 ; Eng. transl., p. 609), I think this sac should be regarded as the bladder which ultimately came into communication with the lumen of the vessel.

[2] See Heller, *loc. cit.*, p. 323 ; Eng. transl., p. 598. Also, Marchand, "Ein Fall von sog. Cysticercus racemosus des Gehirnes," *Archiv f. pathol. Anat.*, Bd. lxxv., p. 104, 1879. I must also note that the irregular form of the *Cysticerci* in the brain was previously known to Helminthologists.

[3] In one of Zenker's cases the patient had also suffered from *Tænia solium*. Heller, *loc. cit.*, p. 334 ; Eng. transl., p. 599.

the wall like the daughter-bladders of *Echinococcus.* According to Heller, these bodies extend with the arachnoid, sometimes into the third ventricle and into the lateral ventricles, and always retain the same racemose appearance.

We cannot doubt that mechanical forces, and especially pressure, exert a determining influence on the shape of the bladder-worms. This may be proved by the ellipsoidal shape of the muscular bladder-worms, which gradually results, as we know, from the original spherical form through the pressure exerted by the muscular fibres in contracting. When such determining factors are absent,[1] and the conditions of growth are the same on all sides, then the normal spheroidal shape is retained.

As the shape of the bladder is determined by the mechanical factors of the environment, so is its size determined by the nutritive conditions. The results of my experimental rearing of bladder-worms proved that *Cysticerci* of equal age were not of equal size in different parts of the body. Even in the same organ there are sometimes larger and smaller bladder-worms side by side, and yet we cannot distinguish them either in age or in phase of development. The size is on an average about that of a pea or small bean, but it is very variable. The larger forms are generally found in the internal organs, in situations especially where their growth is but little hindered, as on the free surface of the viscera (liver and heart) and of the brain. In the ventricles of the brain the *Cysticercus cellulosæ* sometimes grows to the size of a pigeon's egg. In the eye, on the other hand, and especially in the chambers of the eye, the worm generally remains small and stunted.

After the death of the worm, a marked decrease in size at once sets in. The bladder fluid is absorbed, the bladder itself collapses, and the surrounding cyst, unless endowed with unusual power of resistance, undergoes similar changes. In the muscles it assumes the form of a long strip, hardly 2 mm. broad, lying between the fibres, and has a tendinous appearance (Stich). Some traces of the former parasites always persist, even though they be only the remains of the capsule or its calcareous contents, by the action of acids upon which a few hooks may sometimes be seen.

It is not, however, always or exclusively the form and size of the bladder which vary thus in different cases. The head not unfrequently exhibits great differences. This is especially the case in the larger bladder-worms from the brain, of which I saw specimens whose

[1] Dressel once observed at the base of the brain an almond-shaped bladder-worm, and rightly supposed that it owed its shape to the pressure exerted on it by the whole mass of the brain. (*Loc. cit.*, p. 17.)

head-processes when protruded were 2 cm. and upwards in length. In the retracted state, such a head-process is usually coiled in a regular spiral of sometimes three turns. Köberlé, who first described such forms,[1] thought he was justified in erecting them into a species distinct from *Cysticercus cellulosæ* in the form and size of the hooks (*Cyst. turbinatus*). I have, however, convinced myself by accurate comparison that there are no specific differences between the two forms. Probably the excessive length of the body depends on the age attained by the bladder-worm in question (p. 510).

Fig. 301.—Bladder-worm from the brain with a spirally coiled body. (× 12.)

Nor can I recognise the *Cysticercus melanocephalus* of the same author,[2] a species established on the strength of a single form also found in the brain. It seemed indeed to be distinguishable by certain peculiarities in its hooks, but the reports of the author are by no means convincing. As to the erection of a species on the strength of the nature of the head-process, this has as little diagnostic value as the presence of the black pigment which is more rarely seen in the bladder-worms than in the adult *Tæniæ*, but occurs sometimes even in this stage.

The almost countless observations which have been made since Werner's days on the *Cysticercus cellulosæ* of man prove clearly how much attention has been attracted to these structures by the discovery of their animal nature. What was formerly known is so disproportionately little, that it was for long a current opinion that Werner was the first to find bladder-worms in man. The error of this is evident from the fact that in the well-known compilation of Bonetus[3] I find[4] a case observed by Wharton (1679), "de glandulis sanis varias corporis partes occupantibus in milite," which obviously refers to bladder-worms in the skin or muscles. One of these so-called "glands" was cut out by a surgeon, and since it "citra ullum putridum aut corruptum humorem tota ex solida glandulosa atque alba carne constabat,"

[1] Köberlé, "Des Cysticerques de Tænias de l' homme," pp. 22, 29 : Paris, 1861.

[2] *Ibid.*, pp. 25, 30.

[3] "Sepulchretum s. Anatomia practica," p. 1540 : Geneva, 1679.

[4] "Blasenbandwürmer," p. 3.

it appeared to him to furnish proof "dare glandulas adventitias plane sanas, nisi quod in numero partium prænaturalium recenseantur." I formerly expressed the opinion that this case of bladder-worms in man was "perhaps" the oldest known, but I have learned from Küchenmeister[1] that in 1558 Rumler observed in the dura mater and roof of the skull of an epileptic patient certain tumours in regard to which the question arose "num pustulæ illæ morbi Gallici soboles fuerint." Similarly Panarolus in 1650 saw *Cysticerci* on the corpus callosum of an epileptic priest.[2] But, including these cases, the old reports as to bladder-worms are extraordinarily scanty. Nevertheless it seems as though the structures in question had been very generally known to physicians from that time onwards. This may be partly inferred from the statement of Hartmann, the discoverer of the animal nature of bladder-worms in general and of those of the pig in particular (p. 511), who in his last communication[3] speaks as follows:—"Glandia, aut quocunque nomine his affines veniant pustulæ, nidos esse verniculorum, mihi fit veresimile." We need not note how strikingly the supposition thus expressed has been fulfilled.

The importance of these worms from a clinical point of view was probably first noticed in connection with those found in the brain. Since these were found to be present in patients who had suffered from cerebral or mental diseases, it was natural to connect the two, and that all the more since it had been widely recognised[4] since Wepfer's investigations in 1672 that the staggers of sheep and oxen was due to a watery bladder found in the brain. The latter was our *Cœnurus*, whose animal nature was first recognised in Göze's time by Leske.[5] Before Werner's discovery, Göze, along with other observers, such as Morgagni, called attention to the fact that certain "extraordinary diseases of the head" were readily occasioned by *Tæniæ vesiculares*.[6]

The pathological phenomena evoked by *Cysticercus cellulosæ* are very variable, according to the occurrence and position of the parasites. Where they are found exclusively in the subcutaneous connective tissue, or in the musculature of the body, they may be almost harmless.

[1] "Parasiten," second edition, p. 58. Küchenmeister seems to have overlooked the "perhaps."

[2] See for further particulars regarding this case, Küchenmeister's studies on the history of Cestodes, *Deutsches Archiv f. Geschichte der Medicin*, Bd. ii., Heft. 4.

[3] *Ephem. Acad. nat. cur.*, Dec. ii., Ann. vii., p. 58, 1688.

[4] "De Apoplexia," p. 56.

[5] "Von dem Drehen der Schafe und dem Blasenbandwurm im Gehirn derselben als Ursache dieser Krankheit:" Leipzig, 1788.

[6] *Loc. cit.*, p. 249. Among the cases here mentioned, those of Weikard may be referred with tolerable certainty to *Cysticercus cellulosæ*.

The worms inhabiting the cutis may be felt through the skin as moveable tumours about the size of a pea, but cause hardly any discomfort. They come and go almost unnoticed, unless it be that owing to their position on the nates or on the back, or in some other situation where they are exposed to considerable external pressure, their capsular wall becomes inflamed, and results in the formation of an abscess.[1] A spontaneous inflammation caused by the bladder-worms alone is as yet unknown, though in a few cases the infected muscular tissue has exhibited a somewhat reddened appearance. As regards discharge of function, a decrease of muscular strength is the most that has ever been observed.

Those cases, however, in which the bladder-worms inhabit the heart seem more serious. But on superficial positions the worms seem hardly capable of occasioning any marked disturbance; but it is different when they lie under the endocardium, or are fixed as stalked bladders to the valves. In such cases we find to a varying extent symptoms of endocarditis, and such phenomena as valvular insufficiency and stenosis, besides palpitation, impeded respiration, and syncope. Without further proof, such as of course primarily the direct demonstration of bladder-worms under the skin or in the eye, the true nature of these troubles could hardly be determined with any certainty. This is true also of the visceral *Cysticerci*, which excite symptoms that have hardly any special or distinctive pathological character, and that vary according to the position of the worms. In the respiratory organs they occasion asthma, and sometimes even inflammatory conditions; in the walls of the intestine they cause peritonitis, &c.

The disturbances of functions and the pathological changes induced by the bladder-worms of the eye are still more serious. This is true at least of those which have taken up their abode within the eye, for in the outer parts, and when easily accessible, the *Cysticercus* is not peculiarly dangerous. The slight inflammations of the connective tissue which may have been excited by the worm cease when it is removed. In the orbit the *Cysticercus* has been as yet certainly observed only in the anterior division—outside the muscular funnel.[2] The eyeball is displaced by the growing tumour, and the conjunctiva is red and sensitive. The thickness of the capsular wall and the occasional formation of pus may be referred to an inflammatory reaction on the part of the surrounding connective tissue. When the worm is lodged in the depth of the orbit, the disturbances become still more serious,

[1] Perls mentions a case in which thirty bladder-worms were extracted from an abscess. "Pathol. Anat.," Bd. i., p. 80.

[2] See Berlin in "Handbuch d. ges. Augenheilk.," Bd. vi., p. 689.

since in such cases the pressure of the tumour must act on the nerve, causing pain, and impairing vision, if not producing blindness.

Among the different cases of intra-ocular *Cysticerci*, those are certainly least serious in which the parasite occurs in the anterior chamber of the eye. Not only can it be easily extracted, but its presence seems to do little more harm than slightly impair vision, and produce a more or less distinct irritation of the iris.

A *Cysticercus* in the fundus of the eye[1] has disastrous consequences, especially in the subretinal tissue, for by the separation of the retina and induced irido-choroiditis sight is in course of time almost wholly lost. The trouble begins by a slight diminution in the power of vision, but this is succeeded by a limitation or interruption in the field of vision, which afterwards becomes a marked defect. After the lapse of some months or even more, inflammation sets in, which spreads to the front of the eye, especially to the iris, and passes through several slow periodically aggravated stages, until finally a "phthisis bulbi" results. More rarely an acute irido-cyclitis is the issue, and this may culminate in panophthalmitis. A most violent ciliary neurosis is associated with these processes, and persists perhaps for several years. As a rule, the danger of sympathetic inflammation has before this necessitated enucleation. When the *Cysticercus* passes early into the vitreous humour the prognosis is somewhat less serious, especially if the worm be encapsuled, as v. Graefe once observed. In such cases the eye sometimes retains its outer form and a slight power of vision. Usually, however, the retina undergoes separation, and here, too, a gradual irido-choroiditis sets in, which usually ends as above described, but sometimes acquires a more glaucomatous character.

Important and interesting as are bladder-worms in the eye, they are still more so in the brain, where they almost always cause serious trouble. Among the cases collected by Küchenmeister[2] there were only sixteen which were not accompanied by pathological symptoms during life. In six cases the troubles were slight, such as headache, fatigue, lethargy, and giddiness; twenty-four were cases of epilepsy (eleven of which were characterised by psychical disorders); six were cases of cramp, and forty-two of paralysis, of which seven were associated with psychical disorders and ten with apoplexy, while twenty-three were mental disturbances of varying intensity, and occurring partly alone and partly combined with more or less radical nervous diseases.

We are indebted to Griesinger for an excellent discussion of these pathological states, though this has been subsequently somewhat modified by Küchenmeister.[3] The former refers the phenomena to

[1] See the reports of Leber and v. Wecker.
[2] *Loc. cit.*
[3] *Archiv f. Heilkunde*, p. 207, 1862.

two groups, those caused by the wandering of the embryos, and those determined by their permanent residence. The symptoms of the first group are more or less inflammatory (headache, giddiness, &c.), with the subsequent phenomena resulting from irritation and compression of the brain. The patients are then usually induced to seek medical advice. As a rule they also complain of attacks of cramp and of mental disorder, of which the former are in all probability due to the movements of the parasites, contraction of the caudal bladder, and protrusion of the head. The diagnosis is not of course always equally certain; such symptoms might appear without the presence of bladder-worms. Specially dangerous are those attacks of more or less epileptic cramp (without aura), which sometimes occur in later life without obvious cause, and which either appear of a semi-acute character, or rapidly succeed one another, increasing in number and intensity till a very serious cerebral disease results. The mental disorders which sometimes appear along with the epilepsy, or sometimes persist by themselves, are generally of the nature of melancholia or mania. Griesinger asserted that paralysis was a very rare consequence of *Cysticercus*, but this is contradicted by Küchenmeister's generalisations. These paralytic consequences are indeed very varied; they appear often only after a long time; they may be widely diffused or restricted to particular parts; but these differences are of secondary importance, being determined by the number and position of the worms, or by the nature of the affected nervous tissue. We know further that *Cysticerci* in the brain are of fatal significance, not merely because of their presence, but also because they soften the surrounding nervous substance and lead to hæmorrhage, and to other diseases, such as meningitis, hydrocephalus, apoplexy, &c., which again induce other disorders, often of very great extent.

Where paralysis, even of slight character, occurs, the position of the *Cysticerci* is almost always deep down; when they are superficial, other serious disorders ensue. In fact, in the latter case, paralysis results only when the *Cysticerci* form round about them apoplectic areas, or when by their position (say at the base of the hemispheres) and size they are capable of exerting pressure even on the deeper central portions. According to Küchenmeister, on whose authority these statements are mostly made, epilepsy has been observed almost only in those cases where both hemispheres or ventricles, or when unpaired organs, especially the pons and medulla, were infected. The *Cysticerci* on the surface of the brain do not *per se* cause mental diseases, except in cases of hereditary predisposition thereto, but these seem to result especially when the cerebral ganglia, ventricles, and choroid plexuses are attacked either by themselves or along with

other parts of the brain. The intensity and exact nature of the symptoms vary of course enormously. We must not for a moment forget that we have not yet anything like sufficient data to determine with any certainty the connection between anatomical and pathological conditions in this matter. Still less can we understand the physiology of such a connection. Since without further evidence, such as the presence of bladder-worms in the skin or the eye, it is difficult to be sure of their presence in the brain at all, it must be even more difficult to determine the position and distribution of these worms.

As in so many other matters, we must look to the future, in expectation of a deeper insight into the anatomical and physiological facts of the case.

Tænia acanthotrias, Weinland.

Weinland, "An essay on the tape-worms of man," p. 64 : Cambridge, U.S.A., 1858.
,, *Med. Correspondenzbl. d. Würtemb. ärztlichen Vereins*, No. 31, 1859.
,, "Beschreibung zweier neuer Tänioiden des Menschen," *Nova Acta Acad. Cæs. Leop.-Carol.*, Bd. xxviii., Taf. i.-iii.

Only the bladder-worm of this Cestode is as yet known. It is very like Cysticercus cellulosæ, *and lives like it in the muscles and brain of man. It is distinguished by the structure of the hook apparatus, which is composed of a triple circle of from fourteen to twenty-six somewhat slender hooks.*

The first observer, Jeffries Wyman, found it in a Virginian woman, who was infested with *Trichinæ*, and who died of consumption. He regarded it as *Cysticercus cellulosæ*, as did Weinland also, until he discovered the remarkable structure of the hook-apparatus.

The reports made by Weinland on this interesting parasite I am able to confirm, after examination of the only specimen which has been seen in Europe, which was most liberally lent me by the owner, my friend Weinland. I may also add that the head of this, as of the ordinary bladder-worm from the muscles, is rolled up in the receptacle like a snail, and has its apex impregnated with black pigment granules.

The total number of hooks in the specimen I investigated was forty-eight, while Weinland reports the number as forty-two. All three forms of hooks are present in equal number, and the smallest thus occur between every hook of the first row and the adjacent hook of the second row on one side. In spite of the different sizes of the hooks, their points all fall very much on the same line, which is due of course to their being inserted at different levels on the rostellum. The diameter of the latter and of each sucker is about 0·35 mm. The

length of the broad wrinkled body of the worm is estimated by Weinland at about 10 mm. The bladder is as large as in *Cysticercus cellulosæ.*

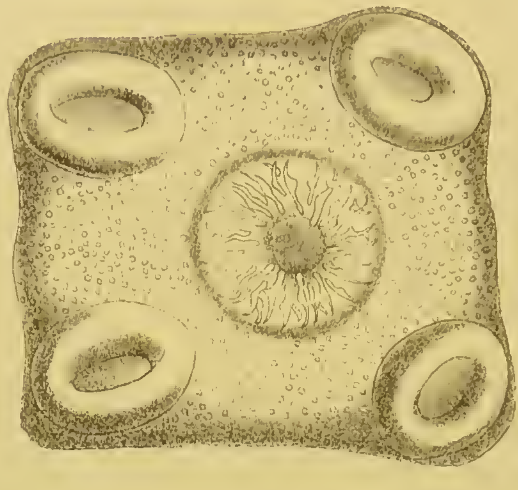


Fig. 302.—*Cysticercus acanthotrias.* Head and circlet of hooks seen from above, after Weinland. (× 60.)

The size of the hooks, according to my measurements, was somewhat larger than according to Weinland. According to me they measured 0·196, 0·14, 0·07 mm., while according to Weinland they were only 0·153, 0·114, 0·063 mm. The length of the roots I estimated at 0·1, 0·07, and 0·035 mm., and the height from the point of the anterior process upwards at 0·1, 0·08, and 0·045 mm. The posterior processes were relatively longer than in *Tænia solium.* The whole form is, as we have seen, somewhat slender, and this applies to the processes as well as to the hooks. The brown coloration of the root-processes is striking, and at one position in the large hooks becomes developed into a distinct black line.

Fig. 303.—Hooks of *Cysticercus acanthotrias*, after Weinland. (× 280.)

This *Cysticercus acanthotrias* represents an independent species, and is not merely a malformed *C. cellulosæ* with supernumerary

circlet of hooks, as has been lately asserted.[1] This is proved not only by the form and size of the hooks, but also by the fact that all the (8-10) specimens yet seen have exactly the same organization. To doubt the value of this character is to question the specific nature of almost every one of the *Tæniæ*.

The worms occurred in a white woman (not a negress) about fifty years of age, and were from twelve to fifteen in number, being all found in the connective tissue of the muscles and subcuticula, with the exception of one, which hung freely on the inner surface of the dura mater, near the crista galli.

The related *Tænia* is unknown, but, from analogy, one is naturally inclined to think that it lives in the human intestine like *Tænia solium*. If this be true, we should look for the bladder-worm also in some other animal, such as the ox.

? Tænia marginata, Batsch.

Küchenmeister, "Ueber die Tænia e Cysticerco tenuicolli, ihren Finnenzustand und die Wanderung ihrer Brut," *Moleschott's Untersuch.*, Bd. i., pp. 256-378: Frankfort, 1856.

The adult Tænia, which is found in the dog and wolf, is distinguished from the other tape-worms parasitic in these animals, first by its length, which attains to 2·5 *mtr., but is usually little above* 1·5 *mtr. The proglottides are also large, and thus it may be easily mistaken for* T. solium, *though the habitat and the form of the hooks are different. The quadrangular head has a diameter of about* 1 *mm. The suckers are, on the whole, smaller and weaker than those of* T. solium; *the hooks are about the same size, but more slender, and provided with longer roots. Their number is on an average from thirty six to thirty-eight, the maximum being forty-two, the minimum thirty-two. The neck is usually so slightly narrowed, that the head passes gradually into the body without perceptible constriction. The segments begin a few millimetres behind the head, but only gradually increase in length, so that the square form is attained somewhat late, at about the time of maturity, and at a distance of about* 50 *cm. behind the head in about the* 550*th joint. The posterior border of the proglottis is prominent, overlapping the anterior edge of the succeeding one, and is not unfrequently undu-*

[1] Thus Redon, '*Comptes rendus*, t. lxxxv., p. 676, 1877. In support of this assertion he cites a case of *Cysticercus cellulosæ* in which he counted forty-seven hooks in three rows (?). The numbers given are somewhat unsatisfactory. Küchenmeister seems to share Redon's opinion ("Parasiten," second edition, p. 136), and would deduce it from a *Tænia solium* with six suckors. It is, however, difficult to see how the brood should come to inherit, instead of six suckers, some forty hooks arranged in three rows.

lating. The last proglottides have the form and size of those in the smaller human tape-worms, having a breadth of 4 *to* 5 *mm., and a length of* 9 *to* 11 *mm. They contain a uterus, which is characterised partly by the shortness of the median stem, and partly by the small number (at most eight) of lateral branches, which have, however, strong and wide-spread ramifications above and below. The embryonic shells are round* (0·036 *mm.*), *thick, and covered by a distinct layer of rods, as in* T. solium.

The worm thus shortly described was first made known to us by Küchenmeister's breeding experiments. He termed it *Tænia e Cysticerco tenuicolli;* after which I showed that it was identical with

Fig. 304.—Hooks of *Tænia marginata.* (× 280.)

the *T. marginata* described by Batsch from the wolf. This Krabbe and Küchenmeister confirmed. The related bladder-worm (*Cysticercus tenuicollis*) lives sometimes alone, sometimes in groups in the omentum, and more rarely in the liver and other viscera, especially of ruminants and swine.[1] It has an oval form, and an appreciable, sometimes considerable, size. In the larger specimens the anterior end of the bladder is drawn out into a long, slender, neck-like process, which bears the parenchymatous worm-body, and encloses it in a sheath, when both are retracted within the bladder. Then it forms a more or less long ribbon, hanging into the cavity of the bladder, in which it sometimes floats freely, or is at certain points connected with the wall.

Fig. 305.—*Cysticercus tenuicollis,* after Bremser (half size).

Since the *Cysticercus tenuicollis* is not a rarity in animals used as food (also in deer and roes), and sometimes grows to the size of a child's head,[2] we may readily suppose that it has been known for

[1] Africa is also a home of the *Cysticercus tenuicollis,* as I have proved by the examination of a *Cysticercus* from *Potamochœrus penicillatus,* for which I am indebted to Dr. Spencer Cobbold of London.

[2] Küchenmeister even credits the bladder-worm with a length "of five feet," "Parasiten," second edition, p. 138.

long. Yet there are but few hints of such knowledge, with the exception of Hartmann, who (in 1685) made his discovery of the animal nature of the bladder-worm in connection with this very form. It is, however, possible that the size and occurrence of this worm have led to its being confused and ranked with *Echinococcus.* This has been a serious source of error, even as regards its human pathology. On the strength of certain cases, partly chronicled by Bonetus and partly the subject of later observation, *Cysticercus tenuicollis* has often been reckoned among the human parasites, especially under the title *C. visceralis.* We must also concede that many of these cases admit of such a construction, as those of Plater[1] and Köplin,[2] where reference is expressly made to *C. tenuicollis.* The identity is never, indeed, certain, so that the occurrence of the latter in man was regarded as a debateable point, as Rudolphi concludes, from the negative results of over a thousand *post mortem* examinations. About twenty-five years ago, however, it became apparently certain that *Cysticercus tenuicollis,* which had meanwhile been observed in monkeys, was also occasionally found in the viscera of man. This was the result of the researches of Eschricht[3] regarding a number of bladder-worms which were collected by the well-known Dr. Schleisner in his observations on the Icelandic liver disease. Among these objects Eschricht found, besides several *Echinococci,* also a *Cysticercus tenuicollis.* There is no question as to the reality of this, but in consequence of Krabbe's results, we are forced to the conviction that there was some confusion or mistake in the sending of the worm in question.[4] In point of fact, the *C. tenuicollis* has never been found in man by the Icelandic physicians,[5] although the *T. marginata* is everywhere the most frequent tape-worm in the dog, and an infection with its eggs could hardly be any more difficult than with those of *T. echinococcus.*

Such being the case, and knowing that *T. marginata* never develops as a tape-worm in man, as has been proved by the experiments made on himself by Dr. Möller in Altona,[6] we might then leave it out of account, were it not that the worm in its Cysticercoid stage is of great interest both to pathologist and zoologist, and affords

[1] Bonetus, "Sepulchretum," Obs. Lib. iii., p. 635.

[2] *Schriften d. Gesellsch. naturf. Freunde,* i., p. 350.

[3] "Undersögelser over den i Island endemiske Hydatidensygdom," *Danske Vidensk. Selsk. Forhandl.,* p. 211, 1853.

[4] "Rech. helminth000g. en Danemark et en Islande," p. 43 : Copenhagen, 1866.

[5] Von Siebold thinks that the liver disease of the Icelanders must be wholly referred to the parasitism of *Cysticercus tenuicollis* ("Band- und Blasenwürmer," p. 113). This statement, however, is erroneous; for even Eschricht, to whom v. Siebold refers, only knew the one case above recorded, and rightly sought the cause of the disease in the *Echinococcus.*

[6] Küchenmeister, *loc. cit.,* p. 319, note.

a good illustration of what we have already said in connection with *Cyst. cellulosæ*, and shall again have to notice regarding the *Echinococcus*.

Further Details regarding the Adult Tape-Worm.

Leuckart, "Blasenbandwürmer," p. 59.
Baillet, "Expérience sur le Cysticercus tenuicollis," &c., *Ann. sci. nat.* (Zool.), sér. 4, t. xvi., p. 99, 1861.
Krabbe, "Recherches helminthologiques," p. 3: Copenhagen, 1866.

In the alimentary canal of the dog there live, besides the above described *Tænia marginata*,[1] two other large-jointed, large-hooked tape-worms, viz., *T. serrata* (e *Cysticerco pisiformi*) and *T. cœnurus* (e *Cœnuro cerebrali*). These do not pass into man,[2] but are, nevertheless, worthy of mention if only because they have so often been confused with one another, and with *T. solium*. The *T. cœnurus*, besides, is among the most dangerous of all Helminths, because its young brood causes the "staggers" of lambs, and thus inflicts great loss upon the farmers. Formerly it was still more common, for we now strive to protect our flocks from being infected by the dogs associated with them.[3]

As to the resemblance which *T. marginata* has both to *T. serrata* and to *T. cœnurus*, this is most marked in the former instance; for *T. serrata* has almost the same external appearance and approximately the same size (it is sometimes over a metre in length). *T. cœnurus*, on the other hand, is full grown at a length of 30 to 40 cm., and, besides this, remains much more slender than either of the others. The chief differences, however, are seen in the structure of the head (*i.e.*, of the hook-apparatus) and of the uterus.

Fig. 306.—Larger and smaller hooks of *Tænia serrata*. (× 280.)

Tænia serrata has by far the largest head (1·3 mm.), the most conspicuous suckers (0·4 mm.), and the strongest armature. The

[1] In the countries where the reindeer abounds *T. Krabbei* is also found (p. 405, note).

[2] The assertion that the *Cœnurus* also occurs in man is based on a misconception, which arose from the unfortunate use which Zeder made of the same generic name (*Polycephalus*) in reference both to *Echinococcus* and *Cœnurus*.

[3] Through the kindness of the well-known breeder v. Nathusius-Hundisburg I am able to state that he has thus reduced the disease from 20 per cent. to from 1 to 2 per cent.

rostellum measures 0·64 mm., and bears a double circlet of from thirty-eight to forty-eight powerful hooks, which (Fig. 306) are fully a third longer and stronger than those of *T. marginata.* The total length of the large hooks is about 0·25 mm., of the smaller 0·14 mm. In the latter, the point of the anterior root is at an almost equal distance from the two extremities (0·084 mm.), while the same distances in the larger hooks are 0·1 mm. in front, and 0·167 mm. behind.

In *T. marginata* the suckers and the rostellum measure about 0·34 mm. On the latter are from 32 to 42 hooks, which in form (Fig. 304) are not unlike those of *T. serrata,* but are less in strength and size, having a length of only 0·19-0·21 mm. and 0·12-0·16 mm. respectively. Specially distinctive are the comparatively great length and the slender form of the anterior processes (compare Fig. 304). This is most striking in the case of the small hooks whose anterior root, as in the related species, has almost a Y-shape. The distances between the two extremities of the hook and of the anterior root are, in the larger hooks, about 0·09-0·1 mm. in front, and 0·11-0·14 mm. behind, while in the smaller they sink to 0·077 mm. and 0·08 mm. Between the hooks one sometimes sees (as also in the *Cysticercus*) isolated black pigment granules, like those of *Tænia solium.*

FIG. 307.—Larger and smaller hooks of *Tænia cœnurus.* (× 280.)

The head of *Tænia cœnurus* is of a more slender, pear-shaped form, with a transverse diameter of 0·8 mm., and with somewhat insignificant suckers (0·29 mm.). The rostellum has a diameter of 0·3 mm., and carries usually twenty-eight (from twenty-four to thirty-two) hooks, of which the larger are 0·16 mm. long, while the smaller measure only 0·1 mm. (Fig. 307). The distances between the extremities of the hooks and the anterior process are in the larger hooks each 0·09 mm., and in the smaller 0·084 mm. and 0·064 mm. respectively. Noteworthy, as being diagnostic, is the heart-shaped structure of the anterior root on the large hooks, and we have also to remark on the smaller and more slender form of the posterior root.

But not only do these three worms differ from one another in their external characters, and in the nature of the hooks, the liberated proglottides also exhibit many differences in size and in the structure of the uterus.

In regard to the differences in size, we must note that *Tænia marginata* liberates the largest and *T. cœnurus* the smallest proglottides. Those of the latter measure (without pressure) 5 to 6 mm. long by 2·5 mm. broad; in the former, the size is almost double (9-11 mm. by 4-5 mm.). The proglottides of *T. serrata* are intermediate in dimensions, and measure 8 mm. by 3 mm.

The structure of *T. marginata* has been already described. *T. serrata* has more lateral branches (8-10 on each side), and a richer and more irregular ramification. In *T. cœnurus* the number ascends to from twenty to twenty-five, but they are somewhat simpler and shorter.

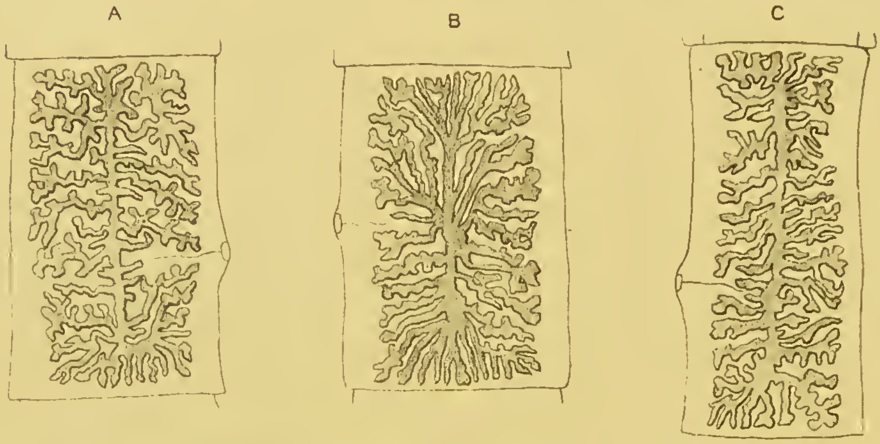


Fig. 308.—Form of the uterus in different tape-worms. *A*, in *T. serrata* (× 4); *B*, in *T. marginata* (× 6); *C*, in *T. cœnurus* (× 10-15).

The eggs of the three species have a somewhat oval form, and are almost equal in size, having a clear average diameter of 0·027 mm. There are of course various divergences in points of detail, and perhaps the eggs of *T. cœnurus* are, on the whole, somewhat larger. The embryonic shell has the familiar appearance, but its thickness, especially in the case of *T. cœnurus*, is markedly inferior to that of the eggs of the human tape-worm. In the size of the embryo and its hooks these species are clearly allied to *T. solium;* in fact all the cystic tape-worms (of the group *Cystotænia*) differ in this respect only in unimportant details.

Of course it is not only the free proglottides which thus differ from one another, but also the "ripe" joints. Their number varies not inconsiderably in the different species, the extremes being again *T. marginata*, with not unfrequently fifty, and *T. cœnurus*, with hardly ever more than a dozen.

It is evident that these differences must contribute to the above-mentioned differences in size of the tape-worms of the dog. But they are not the only factors affecting the latter. We must also

take into consideration the faet that during the development and gradual ripening of the proglottides a more or less extensive growth takes plaec. In *T. marginata* there is between the first ripe joint and the head a ehain of 550 joints, of which the foremost are of very ineonsiderable length. In *T. serrata* there are about 325, and in *T. cœnurus* hardly 200 segments.[1]

I may now pass from the eonsideration of the anatomy of *T. marginata,* espeeially since the charaeter of the internal organs is essentially the same as in *T. solium.* It is true that certain differences in detail are not wanting, of whieh, however, I shall only mention that the muscles of the body (as also in *T. serrata*), are more powerfully developed than is the ease in *T. solium.* Owing to this the contraetility of this tape-worm is mueh greater and more extensive than that of the hook-bearing human tape-worm. The firm appearanee of the chain is also partly due to this eircumstanee.

Structure and Development of Cystieercus tenuieollis.

Like *Tœnia marginata,* whieh is in many respects very nearly related to *T. serrata, Cysticercus tenuicollis* has a great resemblanee to *C. pisiformis.* This is espeeially true of its oceurrence, and, aeeording to my investigations, of the events in its history. At first these bladder-worms inhabit the liver, inside the branehes of the portal vein, which soon after the entranee of the embryos beeome choked through the seeretion of an exuded granular substanee. Few only, however, of the worms remain in this loeality, most of them leaving the liver before the development of the head, to remain for a time free in the body-eavity, and then to beeome eneapsuled anew, generally in the mesentery.[2]

The youngest speeimens of *Cysticercus tenuicollis* hitherto observed are those found by Leisering in a lamb,[3] which died ten days after the feeding. Seen with the lens or with the naked eye, they appeared as "small pale yellow points," whieh lay "in hundreds" in the widely dilated ramifieations of the portal vein. While the surface was still uninjured, they eould be driven out of one vessel into another by eareful pressure with the handle of the sealpel, and when a portion of the larger branehes of the portal vein was exeised, they issued in

[1] These numbers differ from Küchenmeister's statements (according to which *T. marginata* possesses altogether only 400, *T. serrata* 286, and *T. cœnurus* 150 joints), only because the anterior ones, which are certainly difficult to distinguish, have been overlooked.

[2] For further information regarding the developmental history and fate of *Cysticercus pisiformis*, see "Blasenbandwürmer," p. 113.

[3] *Bericht über das Veterinärwesen Sachsens*, p. 22, 1857-58.

great numbers along with the blood. Unfortunately we still lack a detailed description of these young bladder-worms. Not that there is any doubt regarding their nature, for Leisering expressly mentions that closer investigation showed them to be *Cysticerci;* we have only to regret the absence of fuller and more exact statements regarding their size and structure.

In Leisering's case the lamb soon perished in consequence of the feeding, and before the disease had led to inflammation. But that the latter sometimes ensues is shown by the report of Küchenmeister,[1] who made his first feeding experiments with *Tænia marginata*, and always lost his animals with violent symptoms of peritonitis.

I observed a very similar result in the case of a young pig, which was procured from the country for helminthological experiment, but which became infected spontaneously, probably while being brought into the town. The animal began to ail in little less than two weeks, and died some days later. On a dissection being made, the cause of death was found to be a violent perihepatitis. The surfaces of the liver, and especially the concave one, were covered with a thick white deposit, in and under which at least 100 small specimens of *Cysticercus tenuicollis*, with newly formed heads (6-8 mm. in diameter), were embedded. Some were also found free in the body-cavity, and others were encapsuled in the omentum and in the lower parts of the lungs, in which places they had always produced an inflamed circle of about 1·5 cm. in diameter. The intestines, which were matted together into a coil, were strongly injected, and, like the liver, covered in many places with a spotted layer of exudation.

In consequence of this experience, my animals were fed with only a few proglottides, and it is owing to this circumstance that I have never observed in them any symptoms of unhealthiness. On the other hand, of course I found only a small number of *Cysticerci*, never more than eight, and on one occasion only two.

The latter were found in the first animal experimented on, namely, a young pig, which was killed twenty-three days after the feeding. Even on cursory inspection, I saw here and there on the liver a number of white streaks which generally issued directly from the interior, and then sometimes ran for a time below the surface. Most of these streaks were empty, but in spite of their considerable size, I was able to recognise them as worm-passages from the analogy which they presented to similar structures found in the liver of the rabbit after feeding with *Tænia serrata*. Only in two of them there lay enclosed within an egg-shaped distended space a clear transparent

[1] *Loc. cit.*, p. 338.

globule, which, on closer investigation, proved to be a young *Cysticercus tenuicollis*.

The streaks were detached without great difficulty from the surrounding parenchyma of the liver, and proved to be somewhat firm and expansible cylinders, possessing a high degree of elasticity, and consisting largely of a tough granular substance. The length of the cylinders was from about 12 mm. to 15 mm., and their diameter between 1 mm. and 1·5 mm., according to the place at which it was measured. Instead of being regularly rounded, the streaks appeared almost knotted, for they were either thick or thin, either constricted or provided with dilatations, which looked like knots, or with papillary protrusions. Some of these protrusions formed true lateral branches of a conical shape, which, after a short course, terminated in thin solid threads.

I confess that the nature of these structures somewhat puzzled me, until I discovered, while extracting one, that it was connected like a twig with a large branch of the portal vein. The connection was certainly not quite direct, since a short vascular process intervened between the latter and the streak, but although distinctly marked off, it passed continuously into the streak. Under these circumstances, there could be no doubt that the streaks represented modified blood-vessels, so that the *Cysticerci* occupied the same position as in Leisering's case mentioned above.

The histological structure of the knot-bearing streaks was also in agreement with this fact, inasmuch as the cheesy substance which they enclosed contained, besides numerous granules and pus-corpuscles, a number of unmistakeable blood-corpuscles. The dirty white or yellowish walls of the streaks had certainly hardly any resemblance to those of blood-vessels. They were much thickened and of an almost structureless granular nature. At the most, one could only perceive here and there a slight appearance of fibres. I must, however, remark that, on account of its indiarubber-like elasticity, the tissue could only be submitted with great difficulty to microscopic examination.

As has already been mentioned, most of the streaks were untenanted. We must assume, however, that these empty streaks also had inmates originally, but that, as so often happens in such experiments, the worms had perished and disappeared. Only in two streaks had they been preserved and developed into young bladder-worms.

The smaller of the two worms was a delicately walled, clear globule, ovoid in form, and already of considerable size (6 mm. long, 3·5 mm. broad). It lay in an enlargement near one end of the otherwise unaltered streak, and was surrounded on all sides by its granular

contents. Although the head was wanting, the characteristic Cysticercoid nature could be distinctly recognised. Not only did the worm when pricked void a transparent non-granular fluid, but the characteristic structure of the bladder was observable, and showed even the larger and smaller vascular ramifications, with their ciliary lappets. But, in spite of this, there was, as has already been mentioned, no trace of the head.[1] Neither was there any trace of calcareous corpuscles. The latter were also wanting in the second worm, although this was in other respects more fully developed than the former, and was especially characterised by the presence of a rudimentary head.

The length of this second worm was 8·5 mm., and its breadth almost 5 mm. The surrounding tube had, of course, been widened for the reception of so large a body, and, being (Fig. 309) unable to resist the pressure of the growing worm, it had burst along half its length. From this rupture the anterior portion of the bladder protruded like a hernia. So much of the bladder-worm as remained within the case was covered with a tolerably thick exuded layer, the remaining portion being overlaid by a thin layer of connective-tissue.

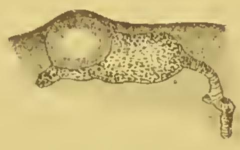


Fig. 309.—Young *Cysticercus tenuicollis, in situ.*

The tube which contained this second worm ran at a short distance below the surface of the liver, and thus the superjacent parenchyma of the liver was almost entirely displaced by the worm as it worked its way out. The connective-tissue envelope of the latter was in contact with the peritoneal covering of the liver, and this was even pushed out into watch-glass-like protrusions by the pressure of the worm.

After the extraction of the bladder-worm, it was observed that both its ends were not exactly of the same shape. The posterior end was rounded, and the anterior conical. It is true that it appeared as though this pointing were, partly at least, due to a contraction of the circular muscular fibres. At any rate, the anterior end of the body exhibited a more opaque appearance and a firmer consistency than were observed elsewhere in the walls of the bladder. The head-process had evidently been formed only a short time before. It was a

[1] These young headless bladders are obviously those which, according to Küchenmeister, "always remain barren," and which he claims to be Acephalocysts of *Cysticercus tenuicollis* (*loc. cit.*, p. 345). Küchenmeister did not know that in this bladder-worm the head is only developed at a later period, and he was somehow under a delusion when he asserted that a cyst only about the size of a tare-seed contained a fully matured *Cyst. tenuicollis.* When, in express reference to my remark, Küchenmeister afterwards declares ("Parasiten," second edition, p. 139) that he must abide by his opinion, since the worms in question were as yet only in "the (atoken = normal) Acephalocystic stage," he forgets that he had previously expressly asserted that they were acephalocysts, "which always remain barren." And it was only against that assertion that my remark was directed.

slender bottle-shaped appendage of insignificant length (1·3 mm.), which hung clapper-like and in a longitudinal direction in the interior of the bladder. The interior of the clapper was of considerable width, especially at the posterior end, but otherwise it had no very distinctive feature. The receptacle appeared in the form of a thin layer, which was in marked contrast to the rest of the head.

In a second pig, which had been fed a month before, the exit from the liver, for which the first case was evidently a preparatory stage, had just taken place. The *Cysticerci*, of which there were four, were found free in the body-cavity. The former streaks had disappeared, but in their place there were seen on the surface of the liver four funnel-shaped pits, of appreciable width and more or less considerable depth, out of which the bladder-worms had issued. The borders of the place of exit were tolerably smooth and not much injected, but deeper down there was to be observed a more or less thick layer of a cheesy substance, evidently the remains of that exuded mass which was found in the tubular streaks, and also in the cysts formed by enlargements of the latter.

The length of the *Cysticerci* was 11 or 12 mm., and the breadth 5 mm. In this case also the anterior end was markedly narrowed, but to different degrees in the different specimens. The head-process had still the same slender form, although its length was now 2·4 mm., and the first rudiments of the suckers and of the circlet of hooks were already distinctly visible on its under end. It is true that both these structures were as yet very far removed from their ultimate form. The suckers appeared simply as hemispherical protrusions on the inferior flask-shaped enlargement of the cavity of the head, and were for the most part still without the subsequent muscular layer, which was differentiated from the surrounding wall only in one specimen. Similarly, the hooks were sometimes represented only by the claws, which, with blunt base, were situated as little cones upon the floor of the cavity of the head; yet, in spite of their softness and the thinness of their walls, they had already attained their subsequent size and form. The calcareous corpuscles within the head were few in number and of insignificant size.

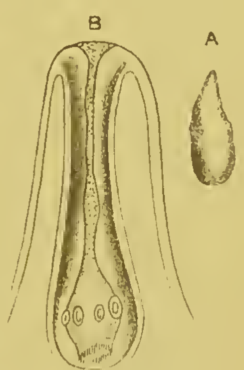


FIG. 310.—*A*, Young *Cysticercus tenuicollis* (nat. size); *B*, the head-process (× 15).

It is hardly necessary to notice specially the differences between the young *Cysticerci* and the muscle bladder-worms, especially of *T. solium.* Apart from the actual history, the differences are indeed marked enough, not only in the size and form of the bladder, but in

the position of the head-process and in the late period of its formation. The straight position of the head lasts, however, only for a short time. After the head is fully developed and its pedicel begins to grow, the head-process in *Cysticercus tenuicollis* (Fig. 311) folds together in the interior of the receptacle, just as in the majority of the other bladder-worms.

Before proceeding, however, to the consideration of the other changes undergone by the worms, I may mention that recently Baillet in Toulouse has, by experimental investigations on *Tænia marginata*, obtained results which are strictly in accordance with the preceding ones. Of these experiments, I shall only make special mention of one which was made on a lamb. The latter received at three different times, between the 4th and 10th of April, one, five, and eleven proglottides of *Tænia marginata* (*T. Cysticerci tenuicollis*, Baillet). It became very ill on the fourteenth day after the feeding, and died towards evening. On dissection there was found in the abdominal cavity a considerable ecchymosis, which originated from the numerous small streaks penetrating the congested liver. Each of these streaks consisted of a tube, whose wall (unquestionably an exuded layer) was easily distinguished from the parenchyma of the liver, and whose blood-filled interior contained from one to four small oval bladders. These measured from 0·6 to 3·5 mm. (or, in the smaller diameter, 0·35 to 2 mm), and, in spite of the absence of a head-process, were with all justice regarded as young bladder-worms. Some of these streaks had opened externally, and had poured their contents of blood and bladders into the body-cavity. Some young *Cysticerci* were also found in the lungs and omentum; in the former situation generally in the centre of a more or less extensive ecchymosis. The whole number was estimated at several thousands.

Thus it will be seen that the result of this investigation fills up, in a very welcome manner, the gap between Leisering's experiments and my own; and as Baillet himself clearly states, gives fresh support to the hypothesis of a wandering occurring through the blood-vessels. Baillet's other experiments yielded much less striking results, and also produced a much smaller number of bladder-worms (19, 1, 8, and 30), although the number of proglottides administered was not less than in the first case.

As to the changes undergone by the worm after the transference into the cavity of the body, I first succeeded in observing them in a young pig, infected seven weeks previously, in which the bladder-worms were about the size of a filbert (15 mm.), and were already encapsuled in the omentum; but that in this case also the original abode of the worms had been the liver, was shown by the fact that its surface

exhibited stellate or linear scars, just like those found in the liver of the rabbit after the exit of *Cysticercus pisiformis*. Besides this, the connective tissue capsules of the mesentery were, on their internal surface, without that granular exuded layer which was usually found in the first breeding-place of the worm. Instead of it there was a layer of slightly granular, clear, and pale balls, which in many respects recalled pus corpuscles, and were about double the size of blood-corpuscles.

I need hardly describe in detail the structure of the head process. It consisted of an opaque mass of nearly spherical form, and 2·4 mm. in diameter, which was in marked contrast to the semi-transparent bladder, and occupied the whole of the anteriorly projecting wart-like summit of the latter. The circlet of hooks, the rostellum, and the suckers were fully developed. The body, closely connected with the head, had a length of almost 4 mm., and a somewhat large transverse section. In histological respects, also, the head had completed its development, as was sufficiently shown by the distinct muscular fibres, calcareous corpuscles, and vessels.

I found bladder-worms in essentially the same condition in a lamb three months after feeding. The only modifications worth mentioning were in the size of the bladder, which, with a breadth of about 12 mm., had now grown to double the length, while in a fresh condition its vessels could be plainly distinguished even by the naked eye. Especially noticeable, as in *Cysticercus cellulosæ* (p. 509), were two irregularly branched longitudinal stems, which ran down from the head-process towards the posterior end of the body, and broke up into an extremely delicate network. The external surface of the bladder was traversed by fine longitudinal and transverse wrinkles, which (perhaps in consequence of the contraction of the muscular fibres lying under them) were closely crowded together. The head-process and receptacle had exactly the previous structure. The former, in its original invaginated state, with its bendings and folds, filled up the interior of the latter. It required a somewhat powerful pressure to expel it, whereupon it of course turned its formerly interior surface outwards, and assumed the attitude of the subsequent tapeworm body. In this state the length amounted to between 5 and 6 mm., and its breadth at the lower end to fully 2 mm.

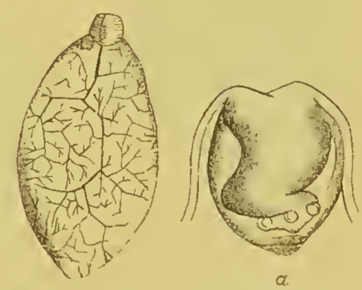


FIG. 311.—*A*, *Cysticercus tenuicollis*, three months old (nat. size); *B*, The head-process (× 10); *a*, rudiment of the ribbon-like process.

From the analogy between these bladder-worms and the related

forms, we might now suppose that it had attained its complete development. But the investigation of older specimens proves the contrary. For not only does the bladder continue to grow until it has attained the size of a goose-egg or more, but the head-process and the point of attachment also undergo further modifications.

The most remarkable is that which has to do with the receptaculum. The posterior end of the latter grows into a solid process, and ultimately forms the above-mentioned ribbon (p. 564), which is to some extent a continuation of the head-process, and hangs down to a variable distance in the interior of the bladder. I find the first trace of this structure in the previously described bladder-worms; sometimes, it is true, only in the form of a flat, hump-like projection, which is situated on the receptaculum (Fig. 311 *B, a*), or rather it is formed out of it by thickening and proliferation of the tissues. Even later, this ribbon, in its histology, is most nearly related to the receptacle. Like the latter, it consists of connective-tissue, which is penetrated by muscle fibres, and contains, besides a few isolated calcareous corpuscles, numerous granular cells. The muscular fibres run principally in the peripheral parts, while the granular cells are deeper down, and are sometimes grouped together into a distinct axial band. Where the ribbon, as sometimes happens, comes into union with the inner surface of the wall of the bladder, the muscular fibres are observed to pass directly into those of the latter. The posterior end is sometimes cleft, and even separated into individual fibres.

Fig. 312.—Longitudinal section through the head of an adult *Cysticercus tenuicollis*, with ribbon-like appendage on the receptacle (after Moniez). (× 20.)

We can only briefly indicate the manifold ways in which this structure has been misinterpreted both by earlier and later observers. Besides, having been occasionally claimed as an intestinal or sexual organ, it was also (unfortunately by myself in 1848) associated with the erroneous theory regarding the dropsical origin of the bladder-worms, and was regarded as the remains of the formerly solid tape-worm body. On the contrary, it appears to be in reality, in physiological as well as in morphological respects, a structure of subordinate importance, and is, in short, only a somewhat unimportant outgrowth of the receptacle—a luxurious growth, similar to that which sometimes originates in certain conditions in plants.

Even before the development of this process, the part of the bladder where the receptacle is situated is generally prolonged into

a kind of neck, and drawn out into a hollow cylinder, which sometimes projects externally (Fig. 310, *A*), and is at other times retracted (Fig. 313), so that the head-process is deeply sunk within the bladder. Although the presence of this process has given rise to the specific name of this bladder-worm, it is by no means a characteristic mark, since it varies very much in development, and is sometimes altogether wanting. I have, for example, seen bladder-worms 70 mm. long, with a neck of the same length, and others in which the neck only measured 5 mm. As a rule, the bladder-worms have long necks (in the two specimens mentioned the neck measured 60 mm. in one case, and 14 in the other); but, on the other hand, the contrary is sometimes observed.

As the bladder-worm grows older, not only do the bladder and the receptacle alter, but the whole head-process undergoes change. For when the head-process has attained a certain size (as in *Cysticercus fasciolaris*), it is protruded from the bladder by evagination, and ultimately assumes the form of a wrinkled and somewhat solid cylinder 1 to 2 cm. in length, and situated at the end of the neck of the bladder. Only the head-proper remains, as a rule, drawn in.

This appendage is, however, visible generally only in those cases in which the neck of the bladder hangs freely outwards. If the latter be invaginated into the interior of the bladder of the worm, the body lies hidden in the interior of this neck as in a sheath. At the posterior end, where it is connected with the base of the sheath, one sees the floating gelatinous band issuing from it, looking as if it were a direct continuation of the body of the worm. The receptacle as such is no longer present. It has apparently been invaginated along with the head, and has probably been used in the progressive solidification of what we have seen to be originally a tubular body.

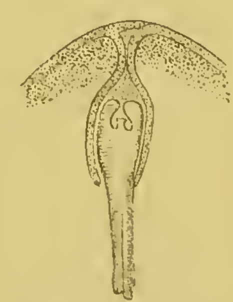


FIG. 313.—Anterior end of *Cysticercus tenuicollis*, with retracted neck, and ribbon-like appendage.

It is not known to what age *Cysticercus tenuicollis* may live, but it appears almost as though it might exist uninjured for many years. At least this may be supposed from the colossal size which the bladder-worm sometimes attains. The Giessen zoological collection possesses a specimen, procured from an ox with retracted neck, which is 160 cm. long and from 6 to 7 cm. thick; and Diesing has reported a specimen taken from a pig, which was almost a foot long,[1] and had a diameter of 4 inches. The true

[1] Could that have been the specimen of "five" feet mentioned by Küchenmeister ("Parasiten," p. 517.)?

tape-worm is, however, of small size, even in such colossal specimens, and is hardly longer than 10-15 mm. even when extended.

The form as well as the size of the bladder is subject to many variations. This is especially true of the ratio between the length and the transverse diameter, which varies so much that the worms are sometimes spherical and sometimes longitudinally extended. Moniez mentions a specimen which was from 6 to 7 cm. in length, but hardly 1·5 cm. broad. Under these circumstances, one might almost guess that the *Cysticercus fistularis* from the horse, described by Rudolphi as possessing a length of 4 to 5 inches and a breadth of 3 to 4 lines, was nothing else than a longitudinally extended *Cysticercus tenuicollis*. In another specimen, Moniez observed at some distance behind the head a rag-like thickening of the bladder-wall, which measured almost 3 mm., and in its histological relations might be compared with a segment of a *Tænia*. I owe to the kindness of Dr. Schmidt in Frankfort a *Cysticercus tenuicollis* of moderate dimensions, whose interior contained three sterile daughter-bladders of 2 to 3 mm. in diameter, and which thus in some respects furnished a counterpart to the *Cysticercus racemosus* already described (p. 554).

In the dog the whole body of the bladder-worm is destroyed after the feeding except the head and its neck. It is true that the solid body of the worm is preserved for a time, and perhaps even longer than in other bladder-worms, but this is not of the least significance to the later Tænioid body. From ten to twelve weeks generally elapse before the expulsion of proglottides, while *T. serrata* only requires eight weeks, and *T. cœnurus* becomes ripe even in three or four.

B. Cystic Tape-Worms, whose heads are budded off from special brood-capsules attached to the inner surface of the bladder.

Subgenus Echinococcifer, Weinland.

J. Müller, *Archiv f. Anat. u. Phys.*, p. 107, 1836; *Mittheil. Verhandl. Gesellsch. naturf. Freunde*, p. 17, 1836.

Von Siebold, Burdach's "Physiologie," Bd. ii., p. 183, 1837.

Huxley, "Anatomy and Development of Echinococcus veterinorum," *Proc. Zool. Soc.*, xx., p. 110, 1852.

G. Wagner, "Entwickelung der Cestoden," *Nova Acta Acad. Cæs. Leop.-Carol.*, Bd. xxiv., Suppl., p. 34, 1854.

Eschricht, "Beretning om fortsatte Undersögelser af Echinokokkerne," *Overs. k. d. Vid. Selsk. Forh.*, p. 127; *Zeitschr. f. d. ges. Naturwiss.*, p. 231, 1857.

Krabbe, "Recherches helminthologiques en Danemark et en Islande," Copenhagen, 1866.

In the cystic bladder-worms of the previous group the tape-worm head originated from a hollow process, which might be regarded as an invagination of the bladder-wall. In the worms of this second

group the heads are developed as before from hollow processes hanging down into the cavity of the bladder, but these processes are not seated directly on the wall of the bladder-worm, but on special small brood-capsules, which attain about the size of a pin's head, and are budded off in ever-increasing numbers from the inner surface of the worm. The cuticle of the bladder, which is distinguished by considerable thickness, does not take the least share in these processes. Sooner or later, sometimes only after complete development, the heads become invaginated into the interior of the brood-capsule, and there become solid. The place of insertion becomes changed into a thin stalk, which encloses the vessels of the tape-worm head. The number of heads becomes continually greater with increasing age, and sometimes amounts to twelve or more in a single brood-capsule. Since the bladder, in contrast to the tape-worm head, has attained a very appreciable size, and often bears many thousands of brood-capsules, the total number of heads is, of course, extremely large. The older heads not unfrequently fall from their stalks, and waste away within the brood-capsule, but this does not counterbalance the new growth. The total number of heads always becomes larger with increasing age. In some cases it may, without exaggeration, be estimated at several hundred thousands.

FIG. 314. — Brood-capsule of *Echinococcus* with retracted head and with two appended buds at different stages. (× 100.)

On the other hand, it must be remarked that the formation of brood-capsules and heads is referred to a later period than is usually the case with the cystic tape-worms. One not unfrequently finds *Echinococci* the size of a pigeon's egg, which as yet contain no brood, and others which remain sterile throughout life.

As to the histology of these animals, besides the above-mentioned thickness of the cuticle, we should also note the extremely sparse development of muscular fibres in the wall of the bladder, in consequence of which the *Echinococci* have no power of vigorous movement. They are as a rule motionless, so that at first sight one might easily take them for simple water-bladders. And this is all the easier, since they are distinguished from the other bladder-worms by very frequently containing (and especially when occurring in man) a varying number of small water-bladders (the so-called "daughter-bladders" or "secondary hydatids"). We shall afterwards return to these structures, and especially to the discussion of their remarkable origin. Meanwhile we shall only mention that in the last case they are the result of a budding, which is not unfrequently repeated in

such a manner that the original *Echinococcus* is changed into a system of cysts enclosed one within another. These resemble vesicles of *Volvox*, to which this parasite has indeed often been compared, and represent so many generations enclosed one within the other, and capable of producing tape-worm heads in the same manner as the mother-bladder. In other cases, as we shall afterwards see, the process of proliferation yields buds, which make their way outwards, and are developed beside, the mother-bladder.

The *Tæniæ*, which are developed from the *Echinococcus*-heads in the intestine of the dog and related animals, are extremely small, and have but few joints; so that in this respect there is a striking difference between them and the cystic tape-worms of the previous group. The hooks are proportionate in size to the head, but are otherwise formed like those of the cystic tape-worms.

Whether there are several species of *Echinococcus* is a question that has been much discussed by investigators. The early helminthologists (with Rudolphi at their head) generally accepted two species, *Echinococcus hominis* and *E. veterinorum*, which differed principally in that the former contained numerous daughter and granddaughter bladders, while the latter consisted usually of a simple bladder. It has long since been proved, however, that the composite form, *Echinococcus hominis*, is also occasionally found in the ox and other mammals (such as the horse, pig, and kangaroo); and, *vice versa*, that the human *Echinococcus* not unfrequently possesses the simple structure of the *E. veterinorum*. Sometimes one even finds two forms of *Echinococcus* side by side in the same individual.[1] It has also been repeatedly noted that it is difficult to differentiate the two forms sharply from each other, since the number of the daughter-bladders varies considerably, being sometimes very large, and at other times limited to a few, so that the compound *Echinococcus* gradually changes into the simple one.[2]

On these grounds many distinguished helminthologists (such as my uncle F. S. Leuckart, Creplin, v. Siebold, and Diesing) have denied that there is any warrant for the separation of these two species, and have explained the indicated differences as mere individual varieties. But at a later period Küchenmeister[3] has again spoken in favour of the old idea, except that he changes the specific names *Echinococcus*

[1] This sometimes happens in the pig, as is shown by Dupuy's case, quoted by Davaine (*Journ. méd. de Sedillot*, t. xcii., p. 63, 1823). In the different muscles, in the lungs, liver, and kidney, *Echinococci* were found, some of which were solitary, whilst others enclosed daughter-bladders within them.

[2] Eschricht mentions a case (of Krabbe's) in which an *Echinococcus* of the size of a child's head only contained two small free-swimming bladders. A counterpart is furnished by those cases in which the number of the endogenous bladders might be estimated at several thousands.

[3] "Parasiten," first edition, p. 139.

hominis into *E. altriciparicns*, and *E. veterinorum* into *E. scolecipariens*. He supports his opinion not only by a reference to differences in the process of proliferation, but also by the statement that both species present decided differences in number, size, and in the form of the hooks. *Echinococcus scolecipariens* has, according to Küchenmeister, twenty-eight to thirty-six hooks of a stouter form, while *E. altriciparicns* has between forty-six and fifty-six, which differ markedly from those of the latter in their slender and elegant structure.

If Küchenmeister were correct in these observations, hardly any objection could be raised against the specific nature of these two forms. But such is not the case: not only does the number of hooks vary in both of them between the two extremes (especially those which lie further from each other, as in most of the other bladder-worms), but the form of the hooks by no means exhibits any decided differences. In comparing the two species, we ought always to go back to equivalent stages of development. But if, like Küchenmeister, we neglect to do so, and compare the tape-worm taken from *E. veterinorum*

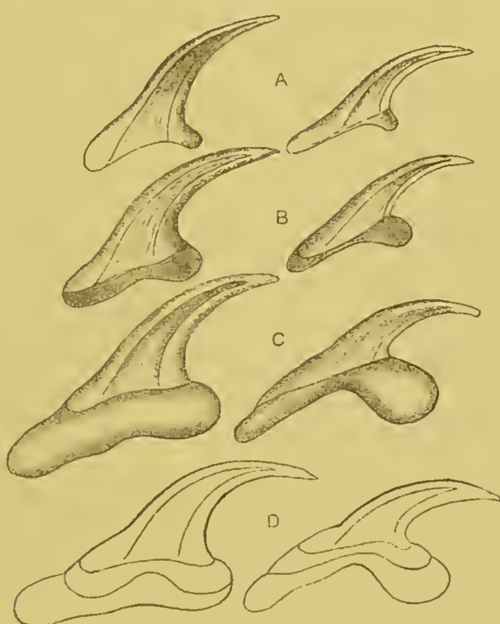


FIG. 315.—*Echinococcus* hooks (× 600). (*A.*) Of *Echinococcus veterinorum*; (*B.*) Of *Tænia echinococcus* in the third week; (*C.*) Of adult *Tænia echinococcus*; (*D.*) The three different hook-forms drawn one within the other to show their gradual changes.

with the rudimentary head of *E. hominis*, we shall indeed see very striking differences of form; but, according to my observations, these differences are to be explained by the fact that the *Echinococcus*-hooks *only attain their full development during the transformation of the*

rudimentary head into the segmented tape-worm. I have established this fact by comparison of the hooks of the *Echinococcus* from the cow with those of the tape-worm from the same parasite, and in unripe *Tæniæ* (of the third week) I found perfect intermediate forms between the structure of the *Echinococcus*-head and the developed *Tænia.*

As is sufficiently shown in the preceding figures, the difference between the hooks of the bladder-worm and those of the *Tæniæ* of *Echinococcus* have to do exclusively with the roots. The structure of the claws is the same in both, but the root-processes are short and slender during the bladder-worm stage, while in the adult tape-worms they are not only considerably longer, but have also a stouter form. Sometimes even in hooks of the same *Tænia* one finds differences in the length and thickness of these processes, and similar differences are to be found in the *Echinococcus*-heads. In rare cases I have seen in the latter an approximation to the form of the tape-worm hooks, *i.e.*, to a more perfect development of the roots.

This late or even secondary development of the hooks in *Echinococcus* brings it to pass that the roots are characterised by an otherwise hardly perceptible variability in size and form. It is only necessary to take a cursory glance at the examples given by Krabbe on the third plate of his memoir on *Echinococcus,* in which there are displayed not less than forty-two figures of large and small hooks, showing how widely the extremes may differ from one another. Many of the forms may indeed be explained as malformations, but the frequent occurrence of others proves them to be normal. If we compare them more closely, we soon see that the deviations consist mainly in the more or less abundant deposit of chitin on the roots of the hooks, through which deposit the latter sometimes increase in length, and sometimes become gnarled and thickened.

With the demonstration of this late development, the most important of Küchenmeister's arguments in favour of the validity of his species lose their cogency, and they were indeed the only arguments which we had to consider in deciding this question, for the above mentioned differences in proliferation were from the first seen to have only a doubtful value.

Such being the state of the case, even in the first edition of this work, I expressed myself most decidedly against Küchenmeister's opinion, and maintained that the various forms of bladder-worm were only varieties of a single species. The proposed change was not only of fundamental importance in reference to our opinions as to the nature and history of *Echinococcus,* but had a further practical importance since Küchenmeister claimed for his two species two different tape-worm forms, differing not only in structure, but also in host.

There were, in other words, two distinct sources, from either of which man might be infected.

Being unable to identify the hypothetical *Tænia* of *Echinococcus altricipariens* with *T. echinococcus,* Küchenmeister maintained on purely theoretical grounds that the former lived preferably in the human intestine,[1] and that thus the *Echinococcus altricipariens,* which is by far the commonest form of the human *Echinococcus,* sprang from a human tape-worm, and was perhaps only rarely brought to us through the dog. My opinion has, however, in course of time, found not only acceptance, but experimental demonstration. This has been supplied by the above-cited observations of Krabbe, to which I may again refer as important completions of my own researches.

Even Küchenmeister has not been able any longer to resist the force of established facts. In the new edition of his work on parasites[2] he concedes with apparent unwillingness that the different forms of *Echinococcus* are but varieties of the same species (*T. echinococcus*).

Since the *Echinococcus*-bladders have almost no power of motion in consequence of the considerable thickness of the cuticle, and the extremely slight development of their muscle-fibres, and since their heads are only recognisable on microscopic examination, we can understand that their animal nature was established somewhat later than was the case with the other bladder-worms, though their existence and medicinal importance were much sooner recognised. Even in Hippocrates we find passages which refer to this *Echinococcus,* and in the writings of the physicians of the sixteenth and seventeenth centuries we find descriptions of the so-called "Hydatids," which give a correct and full statement of the external characters of the organism.[3] Pallas was, however, the first (1767) to recognise in these vibrating hydatids independent organisms allied to the bladder-

[1] We shall afterwards see that Küchenmeister has not even yet shaken himself free from this utterly groundless opinion.

[2] On page 162 he says, "I do not by any means contend that all the varieties of *Echinococcus* represent distinct species of *Tænia.*" For one who formerly maintained unequivocally the specific distinctions between these "varieties," this is a withdrawal without any express acknowledgment of error. The change in the form of the hooks, so characteristic of *T. echinococcus,* receives no further mention, except what we find on page 136, where Küchenmeister, in discussing the question whether the differences in the structure of the hooks between *Cysticercus acanthotrias* and *C. cellulosæ* are sufficient to establish a specific distinction, says, "If the structure of the hooks in the different forms of *T. echinococcus* be considered as varying with the individual hosts, and not merely with their systematic position (*sic!*), the same view might be adopted here."

[3] Other such cases are collected by Pallas (*Neue nord. Beiträge,* Th. i., p. 84), by Leuckart ("Blasenbandwürmer," p. 4), Davaine (*loc. cit.,* p. 350), and by Küchenmeister ("Parasiten," second edition, p. 56, note), and still more thoroughly in the *Deutsch. Archiv f. Geschichte d. Med.,* Bd. ii. u. iii.

worms,[1] while in 1781 the "balls" therein contained were ranked along with the *Cœnurus*-heads which had been just discovered by Leske.[2] The proof of the correctness of this opinion was furnished by Göze, who in 1782 showed that the heads really belonged to *Tæniæ,* and possessed suckers and hook-apparatus, and also soon recognised that they were independent forms, and could not be ranked beside the "white bodies or worms in the brain of the sheep afflicted with staggers," since they were "several hundred times smaller."[3] And this was applied not only to the *Echinococcus* of the cattle, but also to that of man, and that through a specimen which the elder Meckel had sent for closer scrutiny to the indefatigable helminthologist and pastor at St. Blasius in Quedlinburg.[4] Subsequent observers were not all equally successful in their search for these heads, and thus it happened that some even disputed the existence of real *Echinococci* in man,[5] and, like Laennec, regarded the bladders as a special animal organism (*Acephalocystis*) which stood in the lowest rank of animal life, and in a certain sense filled up the gap between the inanimate serous cysts and the ordinary bladder-worms.[6]

In many cases these so-called "acephalocysts" were, indeed, nothing else than hydatid-like pseudoplasms, which had, of course, no connection with animal parasites, and were readily distinguished from the *Echinococci,* not only by their continuous connection with the surrounding tissue, but also histologically and chemically by the nature of their bladder-wall.

Although Bremser in 1821 again proved that the encapsuled *Echinococcus*-bladders of man had heads as well as the so-called *E. veterinorum,* yet, till within a few decades, the old opinion was still maintained, that there were acephalocysts representing a special

[1] *Stralsunder Magazin*, i., p. 81. "It seems to me very probable," he says, "that the incompletely developed water vesicles seen by many observers in the human body, such as those oftenest found in pathological cavities in the liver, are caused by and arise from a worm resembling our own tape-worms (*i.e., Tænia hydatigena = Cysticercus*)."

[2] *Neue nord. Beiträge*, Th. i., p. 85.

[3] "Versuch einer Naturgesch.," p. 158.

[4] This is the same case which gave rise to the above-mentioned opinion that *Cœnurus* occurred in man—an opinion still strangely maintained by Küchenmeister ("Parasiten," second edition, p. 57). It "was for long indeed" generally accepted, until Rasmussen (1865) distinctly proved that it "referred to an *Echinococcus* given by Meckel to Göze, and found among the effects of the latter." Küchenmeister seems to have entirely overlooked the above passage quoted verbally from the older edition of this work.

[5] The word *Echinococcus*, strictly speaking, is applicable only to the head, and was formerly so used.

[6] "Mém. sur les vers viscér. et principal. sur ceux qui se trouvent dans le corps humain :" Paris, 1804.

animal form.[1] This report received strength from the fact that some *Echinococci* have really but few or even no heads in their bladders. This loses all importance, however, when one sees that in the encysted *Echinococci* sterile bladders are sometimes found in the same cyst with proliferating ones. The sterile bladders are, further, not merely smaller, half abortive forms, so that they might be held as immature, but on the contrary, they are not unfrequently the larger.

I do not for a moment doubt that the imperfectly developed *Echinococci* have often been regarded as acephalocysts.[2] From my experimental observations I may consider it as settled that the heads of the *Echinococcus*-bladders are formed much later than those of the *Cysticerci*, at a time when the young worms have already grown to a considerable size. Such immature *Echinococci* must therefore be observed all the more frequently, since the development of these animals takes an unusually long time. The *Echinococcus*-bladders grow for fully four months and more before they are capable of proliferation, and have then attained the size of a small walnut. This is, of course, true only of those worms which develop from the six-hooked embryos: for in the daughter-bladders, and in those budded off on the outside of the mother-cyst, I have sometimes seen brood-capsules of the size of a hazel-nut and less with heads inside them.

The sterile *Echinococci* remain throughout life at an early stage of development. They are like trees which never bear flowers or fruit. In plants, sterility usually depends on the conditions under which they live, and the same may be true of the *Echinococci*. In point of fact, it has been repeatedly observed that in certain localities the *Echinococci* are much oftener sterile than in others, the *Echinococci* of the brain, *e.g.*, more frequently than those of the liver, &c.[3] In man this sterility is not unfrequently associated with the absence of daughter-bladders, which is certainly a renewed caution not to emphasise too strongly the vegetative conditions in judging of specific distinctions. Thus, in a case described by Charcot and Davaine[4] of

[1] See Tschudi, "Blasenwürmer," p. 28. On the other hand, the animal nature of these so-called "acephalocysts" is often distinctly denied, *e.g.*, by Rudolphi, Blumenbach, Heusinger, &c., and for a while by Küchenmeister. But the latter was, as he himself remarks ("Cestoden," p. 6, note), first convinced of his mistake by my demonstration of the chitinous nature of the bladder-wall. And yet he sometimes gets the credit of being the first to establish the true nature of the acephalocysts.

[2] Thus, *e.g.*, by Kuhn, whose figures exactly correspond with the *Echinococci*, four months old, of my rearing ("Rech. sur les acéphalocysts," *Mém. Soc. hist. nat. Strassb.*, t. i., 1830).

[3] On the whole, the importance of these results is but slight, as is evident from the fact that the presence of heads and hooks is noted only in a very small minority of the cases of human *Echinococci*.

[4] *Mém. soc. biol.*, p. 107, 1857.

multiple *Echinococci* in the liver and other visecra, all the cysts which lay under the peritoneal coating of the intestine, and were connected with it only by a more or less long, thin stalk, were devoid of daughter-bladders and heads (or had only very small ones), while all the others exhibited the normal structure.

The rarity of the heads is also the reason why the true nature of the so-called "multilocular" *Echinococcus* was misunderstood, until Virchow's researches.[1] The small component bladders used to be considered as colloid masses, and the whole as an alveolar colloid cancer.

Tænia echinococcus, von Siebold.

Von Siebold, "Ueber die Verwandlung der Echinococcusbrut in Tänien," *Zeitschr. f. wiss. Zool.*, Bd. iv., p. 409, 1853.

A tape-worm of comparatively small size, and with only three or four joints, of which the last, when mature, exceeds all the rest of the body in size. The total length is only a few (at most 5) *millimetres. The small hooks have stout root-processes, and are seated on a somewhat swollen rostellum. Their number usually amounts to some thirty or forty.*

The young stage, long known under the name *Echinococcus*, forms a very conspicuous, almost motionless bladder, with a thick, elastic, and frequently laminated wall, on whose inner surface, in special brood-capsules of the size of a millet-seed, there are budded off numerous small heads, almost invisible to the naked eye. Not unfrequently the bladder increases by budding either externally or internally; it may thus become a composite system of larger and smaller bladders, one within the other. Such bladders are found especially in man and the ox, while other ruminants—swine and monkeys—usually harbour either simple bladders, or those with exogenous multiplication.[2] The favourite place for the *Echinococcus* is the liver or lungs; but there is hardly an organ which may not harbour it. The adult tape-worm lives socially in the intestine of the dog, jackal (Panceri), and wolf (Cobbold).

Description of the Adult Tape-Worm.

The head of *Tænia echinococcus* is characterised not merely by its small size (its transverse diameter is scarcely 0·3 mm.), but also by

[1] *Verhandl. d. med. phys. Gesellsch. z. Würzburg*, Bd. vi., p. 84, 1855.

[2] With the exception of the peacock, in which an *Echinococcus* was detected by v. Siebold, and lately again by Pagenstecher, mammals are the only hosts of this worm. I may here mention as well the occurrence of an *Echinococcus* in the liver of a squirrel, which I found noted in one of my uncle F. S. Leuckart's papers.

the possession of a somewhat prominent crown (0·13 mm. broad) which surrounds the bulging rostellum. The hooks borne by the rostellum form, as in the other cystic tape-worms, two series of from

FIG. 316.—Adult *Tænia echinococcus.* (× 12.)

FIG. 317.—*Echinococcus veterinorum* (nat. size and position).

fourteen to twenty-five each, but they are rarely found in a perfect state. The hooks are characterised by the thickness and solidity of their roots (Fig. 315, *C*). In details they vary widely even in the same worm.

Those of the inner series are, as usual, the larger, and when full-grown attain a length of 0·04 to 0·045 mm. More than half of this is formed by the roots; the distance of the point of the anterior root from the posterior end is 0·025 to 0·028 mm., and from the anterior end only 0·017 to 0·019 mm. The claw is slender, and somewhat strongly curved. The roots appear somewhat thicker and stouter, inasmuch as the saddle-like notch between them is often more or less completely filled up. The back of the posterior root not unfrequently shows in the middle a shallow, curved cleft. The hooks of the second series are not only smaller (0·030 to 0·038 mm. long), but have a thinner posterior root, compared with which the markedly projecting anterior root has an almost discoidal form. The distance of the end of

the anterior root from the point of the hook is 0·013 to 0·015 mm.; from the posterior end of the hook, 0·022 to 0·025 mm.

Behind the four[1] plainly muscular suckers (0·13 mm. in diameter) the head narrows to a neck about 0·25 mm. thick, which then passes without distinct boundary into the unsegmented anterior part of the body. The first segment is but faintly marked off, being scarcely broader than the preceding portion of the body, and almost as long as broad. In the second segment the breadth has been doubled, and the length increased four times, while the male and female reproductive organs can be distinguished—a peripheral cirrhus, a vas deferens, and eggs which collect in the uterus in the middle of the joint, and sometimes already exhibit the first signs of embryonic development. The third and last joint exhibits all the characters of maturity. It has not merely grown to be 2 mm. long by 0·6 mm. broad, but is also provided internally with hard-shelled eggs, which enclose the familiar six-hooked embryos, and, according to the computations of Johne and Küchenmeister, are about 500 in number.[2] In isolated eggs one can distinguish, besides the hard shell, also the outer clear egg-membrane, which is so distant that the total diameter is 0·065 mm. The form of the uterus is moderately simple; one can recognise a wide median stem, with several diverticula or short, slightly ramified lateral branches. In spite of the minuteness of the tape-worm, the eggs have the ordinary size, but the shell is comparatively thin, and is but faintly granulated on the outer surface. The internal space is oval, and has a transverse diameter of from 0·03 to 0·027 mm. The cirrhus of the ripe joint is usually directed to the opposite side from that of the preceding, so that *Tænia echinococcus* agrees with the other cystic tape-worms in the irregularly alternating arrangement of the generative openings.

Before this last ripe joint is liberated, a new joint appears; so that for a while four proglottides are distinguishable, instead of three.

The calcareous corpuscles are somewhat large, and, in the more transparent anterior part of the body, are easily found. In fresh specimens the course of the vessels can usually be seen very beautifully. Von Siebold even mentions the ciliation which is observable in the anterior of the body-parenchyma, behind the suckers, at the sides of the neck and body.[3]

[1] Von Siebold once saw a *T. echinococcus* with six suckers (*loc. cit.*, p. 425). Nothing was noted as to the structure of the segmented body. The fact that this malformation has been seen only in one specimen is in favour of the opinion we previously expressed as to its spontaneous origin.

[2] My previous estimate (4000 to 5000) is too high.

[3] Two memoirs, which have appeared while these sheets were passing through the press, establish beyond cavil the repeatedly denied existence of a ciliary apparatus in the

The Sexual Organs of *Tænia echinococcus* exhibit many striking peculiarities, which, when compared with those of other tape-worms, contribute not a little to justify the independent position which we have claimed for it here.

The Male Organs strike one by the unusual size of the cirrhus-pouch, which measures almost 0·5 mm., and, by its club-shaped, thickened posterior end, reaches to the middle line of the newly fertilised joints. The cirrhus itself has apparently a greater independence than is the case in the other cystic tape-worms. It lies in the anterior portion of the cirrhus-pouch, like the glans in the præputium, and is not unfrequently protruded. Sometimes it is found in the act of copulation. The sexual cloaca is destitute of a proper papilla, the penis itself is bent into a sort of hook-shape, and is sunk into the anterior end of the adjacent vagina.

Before its entrance into the posterior end of the cirrhus-pouch, the vas deferens makes several irregular coils, which are mostly distended with spermatozoa. In the testes, too, the spermatozoa are readily recognisable since they possess an unusual length and thickness. They are usually seen rolled up in curls, and can sometimes be observed passing into the thin efferent canals of the testes. The size of the testes is quite appreciable, averaging about 0·07 mm., and their number is proportionately reduced to about sixty.

The Female Organs.—The vagina is characterised by a longitudinal enlargement (with a transverse diameter of 0·05 mm.) in the middle of its course. In this there can be seen a yellow chitinous lamella, with numerous points directed outwards. It is the same structure which we noted in the other cystic tape-worms. Its posterior end leads to a distinct bladder (0·014 mm.), whose contents con-

vascular system of Cestodes, and furnish also an almost exhaustive examination of the latter system. The two memoirs are (1.) by Fraipont, "Réch. sur l'appareil excreteur des Trématodes et Cestoides," *Archives de Biol.*, t. i., p. 415 ; and (2.) by Pintner, "Untersuchungen über den Bau des Bandwurmkörpers," *Arb. des Zool. Instituts zu Wien*, Bd. iii., 1880. According to the harmonious results of both, the cilia are never found in the course of the finer vessels, but only at their ends, and that in a sort of funnel-like enlargement, as was already known in part in regard to the Trematodes, having been demonstrated by me in 1863 on the embryos of *Distomum hepaticum* (first German edition of this work, Bd. i., p. 766). The funnels contain each only a single cilium, and this belongs to a cell which shuts the mouth of the funnel like a lid, and was regarded by Pintner as a gland-cell. The fine vessels pass out from the funnels, open without marked enlargement either alone or in groups, and often after ramification, into the longitudinal vessels. The latter never ramify, but are clad externally with an epithelium-like cellular coating, which has probably a secretory character. Besides the existence of the ciliary apparatus, that of the nervous system has been established by Pintner. The researches of this young investigator refer primarily and principally to the *Tetrarhynchi*, which have less interest for us here, although alluded to above (see p. 295) ; but there are many references to the Tæniadæ. The reports on the finer anatomy of the tape-worms are in beautiful harmony with my results, though there are divergences here and there.

sist of spermatozoa,—in other words, into a receptaculum seminis. Opposite the opening of the vagina there rises from this receptaculum a fertilising canal of appreciable width, and distinguished by the double contour of its walls. After a short course, this divides into two narrower ducts, of which the one bends forwards, while the other continues the original course backwards. The former of these two canals is the oviduct whose upper end is connected as usual with the two ovaries.[1] The cæcal tubules which form the glands are short and wide, and so slightly separated that the ovaries look more like lobulated sacs than aciniform glands. Internally, the eggs may be recognised as sharply defined balls about 0·01 mm. in size. The second canal divides further down into two ducts — one of which enters the simple sacular yolk-gland, while the other is probably in connection with the uterus. The latter appears from the first as a wide cavity. It is somewhat late before it is distinguishable, namely, after the ovaries have liberated their contents, and, like the yolk-glands, have disappeared. I have not been able to find a shell-gland in *Tænia echinococcus*.

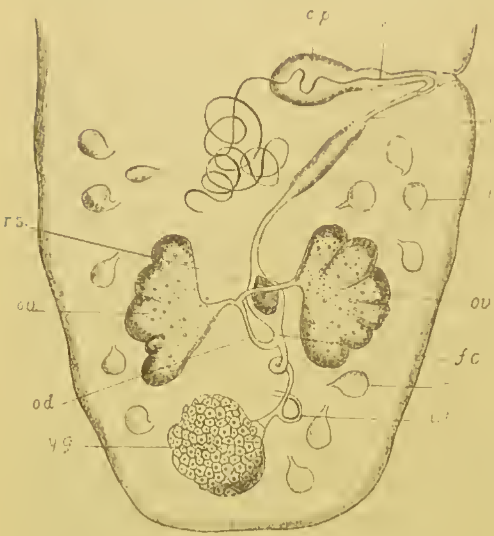


Fig. 318.—Generative organs of *Tænia echinococcus*. Male organs—*t.t.*, testes; *c.p.*, cirrhus-pouch; *c.*, cirrhus, curving round to enter the vagina. Female organs—*ov.*, ovary; *o.d.*, oviduct; *r.s.*, receptaculum seminis; *y.g.*, yolk-gland; *ut.*. tube, probably leading to the uterus; *f.c.*, fertilising canal; *v.*, vagina. (× 80.)

Situation and Habits.—This worm usually occurs in considerable numbers, sometimes in many thousands, between the villi of the small intestine, so that only the milk-white ripe proglottides project. When the latter are not present, the worms can hardly be recognised with the naked eye.

In the still warm intestine they exhibit lively and striking movements. They elongate and shorten their joints, especially the first, and move forwards in the surrounding intestinal mucus quickly and powerfully, almost like leeches. Sometimes the body becomes so thin that they almost resemble Nematodes.

[1] The narrowness and general nature of the transverse efferent ducts of the ovaries exclude the possibility (maintained by Sommer in regard to the other cystic tape-worms, see p. 444) that they are glandular lobes.

According to v. Siebold's investigations, the metamorphosis of the *Echinococcus*-heads into these tape-worms takes place with great rapidity. Fifteen or twenty days after feeding he found on most of the heads a two-jointed body, while others (the majority, according to one of my experiments) were still without segmentation. Thereafter three joints appeared, and some days later (on the twenty-seventh after feeding) some hard-shelled eggs with embryos were found in the last joint. Van Beneden also saw the *Echinococcus*-heads becoming ripe *Tæniæ* within four weeks after feeding, while Küchenmeister, who experimented at the same time as v. Siebold, discovered no ripe forms for eight to nine weeks. In my experiments I did not find mature worms till the seventh week. Zenker, even eleven weeks after feeding, found them perfectly developed as regards size, but still without eggs.[1] In the feeding experiments of Naunyn, Pagenstecher, and Nettleship, seven weeks were also required for the attainment of maturity.

FIG. 319. *Echinococcus* before the beginning of the segmentation (× 15).

We do not know yet how long the tape-worm lives, but the insufficiently supported supposition of v. Siebold, that they did not survive two months, can hardly be correct; for not only does the form and thickness of the roots of the hooks suggest in certain cases a greater age, but we cannot suppose, against all analogy, that the productivity of the worm is exhausted after the one or two proglottides. Further, we must remember that the *Tænia echinococcus* is, like the other cystic tape-worms of the dog, found much more frequently in older animals than in those still in the first year of their life.

Tænia echinococcus was repeatedly observed before the researches of the above-mentioned investigators. It was noticed apparently by Rudolphi, who found it in immense numbers in a pug-dog. Its attachment between the intestinal villi and its small size led, however, to the supposition that it was the young of the common tape-worm of the dog (*T. cucumerina*), which had just arisen by generatio æquivoca.[2] The villi were supposed to pass directly into tape-worms. Later observers also considered these worms as young forms of other species. Thus Röll claimed them as young stages of *T. serrata*, and Diesing was inclined to refer the specimens collected by Natterer from a puma (*Felis concolor*) from Brazil to the large-hooked tape-worms of the cat (*T. crassicollis*), and this, too, in spite of the expressly noted ripeness of the last joint. Van Beneden in 1850 was the first to recognise an independent species in this worm, which he described

[1] *Sitzungsb. d. med.-phys. Gesellsch. Erlangen*, p. 88, 1872.

[2] "Entozoor. hist. natur.," t. i., p. 411, 1808.

as *T. nana*,[1] and, anticipating subsequent discovery, sought to refer it to *Echinococcus*.

It is doubtful whether the worms collected by Natterer from *Felis concolor* belonged to the same species as our native *Echinococci*. It is, however, certain that our domestic cats are but little adapted for rearing the *T. echinococcus*, as I have convinced myself by repeated feeding experiments. I have also experimented in vain with rabbits. Although v. Siebold remarks the same in regard to the fox, which also belongs to the genus *Canis*, the dog is not by any means the only host of *T. echinococcus*. We know, through the observations of Panceri, that it occurs in the Egyptian jackal, and Cobbold notes that it is also harboured by the wolf.

Of course *T. echinococcus* is not only observed in dogs which are made the subjects of experiment, but occurs of itself spontaneously, and in some districts not unfrequently. In Iceland Krabbe observed it in 28 out of 100 dogs; in Denmark, on the other hand,[2] only twice in 317, *i.e.*, only 0·6 per cent. The conditions of life are nowhere else so favourable as in Iceland, where the *Echinococcus* is almost of common occurrence in men and cattle.[3]

That the *Echinococcus* of man produces in the dog's intestine the very same tape-worm as does the so-called *E. veterinorum*, follows from the proof of the specific identity of these two formerly distinguished forms. Nevertheless, the first feeding experiments (of Küchenmeister, Zenker, and Levison) yielded at first only a negative result. The reason of this lay perhaps in the nature of the material used, which, when obtained from the human corpse, is seldom so fresh and well preserved as that from the ox, and partly also in the individual conditions of the animals experimented on. For it does not always happen, as v. Siebold has shown, that they are suited for the rearing of the *Tænia* from the *Echinococcus*. Later investigators have been more fortunate. Thus Naunyn gave to two dogs the contents of an *Echinococcus* from the liver, procured by tapping. One of them exhibited, after thirty-five days, numerous *Tæniæ*, 3-5 mm. long, and with eggs in their terminal joints. The other dog was examined eight

[1] "Mém. sur les vers intestin.," p. 158 : Paris, 1858. Küchenmeister ("Parasiten," second edition, p. 162, note) severely reproaches "the zoologist" v. Siebold, because in 1853 he did not know that *T. echinococcus* had been in 1850 described by "the zoologist" van Beneden as *T. nana;* but the reproach is as unjust as it is frivolous, since van Beneden's memoir, presented in 1852 to the Paris Academy, was only published in 1858.

[2] Similarly, in Giessen I only observed *Echinococcus* in the subjects of my experiments, while from Göttingen the intestines of dogs infected with them were several times sent to me.

[3] [Thus it appeared formerly. I have recently learnt from Thomas ("Hydatid Disease," p. 191 : Adelaide, 1884) that in South Australia no less than 40 per cent. "of the unregistered dogs" are infected by *Tænia echinococcus.*—R. L.]

days sooner, and was without *Tæniæ.*[1] Krabbe also thrice obtained a positive result in the experiments carried on by him and Finsen.[2] The animals used were all young and had lived under conditions which excluded the possibility of a spontaneous infection, and were seen on dissection to be free from *T. marginata* and *T. cœnurus,* which so commonly occur beside the *T. echinococcus* in the Icelandic dog. In five of the animals used no young *Tæniæ* were to be seen, but this negative result probably finds its explanation in the fact that the hydatids used for feeding were not always first examined to see if there were heads present, and were further, in some cases, used several days after the death of the host. The tape-worms found exhibited a development and hook-formation corresponding to the period of feeding, so that the cogency of the experiments can hardly be doubted although they were made in Iceland in a country where *T. echinococcus* is extremely prevalent.[3]

While Küchenmeister still maintained the specific distinctness of the human *Echinococcus,* and was forced, therefore, to regard the *Tænia* arising from the latter as different from the *T. echinococcus,* he advanced the hypothesis that the tape-worm of the first occurred not only in "dogs and cats," but specially in man himself, "in the intestine of those individuals who suffer or have suffered from the corresponding species of *Echinococcus* in any part of their body, and in whom one of these *Echinococci* has opened into the intestine."

If this were indeed the case, then the existence of this *Tænia* could hardly have escaped the investigations of the pathological anatomists. In the new edition of his work on parasites, Davaine cites no fewer than forty cases of *Echinococci* which had opened into the intestine. In no case, however, was a *T. echinococcus* found, nor was it so in any of the forty-five cases cited by the same author in which the *Echinococcus*-bladders opened into the bronchi, and in which their contents had been coughed up. Küchenmeister objects to the relevancy of the question since the *Echinococcus*-heads did not reach the stomach, but he forgets that the above conditions could hardly occur without some portions of the *Echinococcus* being swallowed, and that it is far more likely that the organism should be infected through forms already in the mouth, than with forms that have first to be brought into the mouth from outside.

Although Küchenmeister does not regard my objection as valid, and still keeps to his former opinion, in regarding man as well as the

[1] "Ueber die zu Echinococcus hominis gehörige Tænia," *Müller's Archiv f. Anat. u. Physiol.*, p. 412, 1863.

[2] *Loc. cit.*, pp. 49-52.

[3] [Thomas refers to two feeding experiments with *Echinococcus hominis,* both of which yielded positive results (*op. cit.*, p. 205).—R. L.]

dog as the presumptive host of *Tænia echinococcus*, yet we may all the more readily leave the matter without further discussion since the supposition in question is entirely hypothetical, and supported by no facts whatsoever. We may confidently leave it to the future to discover whether the *T. echinococcus* is found in the intestine of Australian shepherds or of the inhabitants of any district where the *Echinococcus*-disease is epidemic; till then we must be contented with the related bladder-worm stage.

I must take this opportunity of noting that, according to Leisering,[1] the *Tænia echinococcus*, if occurring abundantly in the intestine of the dog, sometimes occasions states which are in their external symptoms so like hydrophobia that they could hardly be distinguished from it.

Development of the Echinococcus-Bladder.

Leuckart, *Göttingen Nachrichten*, Jan. 1862, or, in more detail, first German edition of this work, p. 342.

Naunyn, "Entwickelung des Echinococcus," *Muller's Archiv f. Anat. u. Physiol.*, p. 612, 1862.

The experiments made by Haubner and myself, in which we fed lambs, sheep, and goats with ripe proglottides, remained without result. The dissection was made sometimes soon, sometimes at a longer time, after the feeding, but an *Echinococcus* was never found, although we observed that the liver, and in many cases the lungs also, were penetrated by small white points like miliary tubercles, which could only be caused by the entrance of the young brood.

All the greater was my joy when I afterwards discovered that the pig may be very readily infected by the eggs of *Tænia echinococcus*. The four experiments which I made upon this animal were all successful, and have enabled me to establish a series of facts which will always serve as the starting-point for further experiments. That I have not traced to its close the life-history of the *Echinococcus*, is due to the fact that I have of late lacked the necessary materials.

Fig. 320.—Young *Echinococcus*, four weeks old, escaping from the capsule. (× 50.)

In the first of my experiments the young pig was examined four weeks after the feeding.

[1] *Bericht über das Veterinärwesen Sachsens*, Jahrg. x., p. 87, 1867.

If developed at all, the young *Echinococci* ought, according to my calculations, to have already measured several millimetres, but I sought in vain in the liver, lungs, and other organs for any such structures. The only phenomena which I could at all connect with the experiment were some small knots resembling tubercles (perhaps 1 mm. in size), which shone through the serous covering of the liver in various places. When on the point of concluding that I had again experimented in vain, I discovered in the interior of these knots a spherical body like a bubble, which, in spite of its insignificant size (0·25-0·35 mm.), could be nothing else than a young *Echinococcus*.

When I first saw it, I almost believed it to be a mammalian egg. A thick, homogeneous, and transparent capsule (0·02-0·05 mm. thick), enclosed somewhat coarsely granular contents,[1] just as the zona pellucida encloses the yolk granules. And just as the mammalian egg lies embedded in the cells of the discus proligerus, the outer surface of the clear capsule was surrounded by a substance, in which, upon closer investigation, one could also discern a cellular texture.

Nothing suggested that it was an animal that lay before me. Being motionless, and devoid of any trace of internal or external organs, it would have been difficult to recognise it as a parasite, if the circumstances under which it was found had not emphatically settled the point. For the previous feeding, and the encapsulation of the cysts, which in every respect corresponded to a *Cysticercus*-bladder, placed the nature of the body beyond a doubt, especially since the appearance and nature of the external envelope, in spite of the indistinctness of the lamination, recalled in a very striking way the cuticle of the adult *Echinococcus*.

The boundary of the outer wall appeared, as a rule, somewhat sharply defined, but there were some, especially among the larger specimens, in which the border was less distinct, as is also sometimes the case with the zona of mammalian eggs. It was but slightly affected by reagents, as though it already possessed the chemical nature of the later bladder-wall. Its physical nature seemed also identical with that of the later. It was extremely expansible and elastic, so that the diameter of the bladder could be increased by pressure to more than double. No structure could ever be observed in the "zona."

If left long in water the zona became separated here and there

[1] Naunyn (*loc. cit.*) describes in a similar manner the youngest *Echinococcus* found by him in cattle. "They exhibited," he says, "a bladder of about $\frac{1}{20}$ of a line in diameter, whose wall already showed the structure characteristic of this bladder-worm. It was comparatively thick, and displayed a tolerably distinct concentric lamination. The bladder was filled with small balls like tubercular granules, or with a fluid in which numerous fat-drops were suspended. The latter appeared, however, to be due to a fatty degeneration that had already set in."

from the contents. It was then seen that the latter consisted, like the yolk, of a clear granular matrix, which contained numerous fatty, shining, coarser granules. The distribution of the latter was somewhat irregular, inasmuch as they were more numerous in the periphery than in the interior. For the same reason, the central contents appeared clearer than the peripheral ones, but this was the only point in which they differed. The contents of the zona were thus still perfectly solid, for no formation of fluid had yet set in.

The cells, which lay above the young *Echinococcus*, formed a thick envelope, whose separate elements were so indistinctly defined that at first sight it looked like a continuous granular substance. The size of these cells was somewhat large, on an average about 0·027 mm. Each of them contained a clear vesicular nucleus, from 0·007 mm. to 0·012 mm. in size, in which there were usually embedded two or three distinctly defined nucleoli. Sometimes I found cells with an oval or elongated nucleus, or even with two nuclei, which were at a variable distance from one or other. In the latter case the cellular mass was usually constricted between the nuclei. There is thus no doubt that the cells of this enveloping layer undergo active division, in exactly the same way as I have observed in other bladder-worms, and especially in those of the liver.

As to the connective-tissue cyst which enclosed the *Echinococcus* and the enveloping substance, it was only of insignificant thickness, and was everywhere in direct continuity[1] with the connective-tissue trabecular network of the liver. We can hardly be wrong in supposing that it originates principally from the latter by local development and proliferation. In all cases, moreover, it was the interlobular tissue that contained the parasites. The number of these amounted to from four to six dozen, but none were found in any other situation.

If, however, any uncertainty had existed regarding the nature of the bladder we have described, the case of the second pig, which was killed four weeks later—*i.e.*, eight weeks after the feeding—would have most certainly removed it. The liver of this one was most certainly studded with *Echinococci*, but they had in the meantime grown on an average to double the size of the previous ones. Even with the naked eye this increased size could be perceived, for the young *Echinococci* shone through the enveloping walls like clear drops.

The cysts had of course also grown in proportion to, although much less than, the parasites. Only in a few did the diameter exceed 1·5 mm., and that always in those whose inmates had also attained

[1] According to Naunyn, a distinct connection can be proved between these cysts and the wall of a vessel. "It thus appears," remarks this author, "as though the embryos of *Tænia echinococcus* were distributed through the vascular system."

more than the average size. As in the previous case, the cysts were exclusively confined to the interlobular spaces, although their number was much greater, and amounted to at least from 100 to 120. It is remarkable that the cysts were all thickly distributed under the serous covering of the liver, and that upon both the concave and eonvex surfaces.

The smaller *Echinococci* (of 0·5-0·8 mm.) eorresponded in structure with those found in the first experiment. The only differenee perceptible on superficial inspection was that the eontents of the zona were appreeiably clearer than before. This inerease of transparency was due to a partial liquefaction of the eontents. The *Echinococcus*, which was formerly a solid mass, had meanwhile become a bladder, which, when pricked, voided a portion of its contents in the form of a transparent fluid, and then collapsed.

The fluid had eollected in the centre of the spherical body, so that below the zona a seeond membrane could be distinguished, which lay along the inner surface of the latter, and is to be regarded as a membranous expansion of the real body-parenchyma ("germinal membrane," Huxley, "Keimhaut," Naunyn). The zona itself appeared as a cuticle, and was distinctly lamellated, as we have already noted in

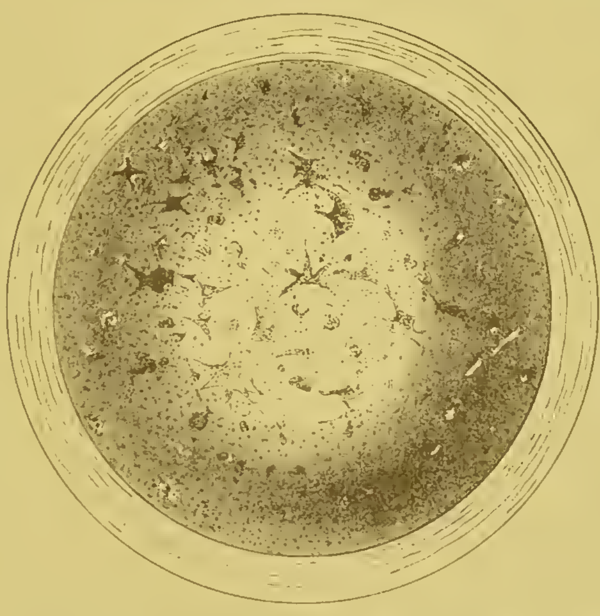


FIG. 321.—*Echinococcus*-bladder eight weeks old. (× 50.)

the adult *Echinococcus*-bladders. But the lamellæ were as yet neither very distinct nor sharply defined, although the membrane sometimes attained a thickness of 0·07 mm. The inner membrane elosely adjoining the eutiele exhibited, besides the granules formerly present, some cellular structures, which presented many differenees in

size and appearance (sometimes measuring as much as 0·028 mm.). Most of these were pale and delicately outlined, and to some extent like drops, but there were others which were remarkable for the granular nature of their contents, and there were even granular cells of considerable size, not unlike pus corpuscles. In the larger *Echinococci* the latter sometimes exhibited stellate ramifications and a clear nucleus which shone through the granular substance. In these large *Echinococci* (there were some specimens of from 2 to 2·5 mm.) it was seen that the different kinds of cells exhibited a definite arrangement. Most externally lay the small cells, and further inwards the large drop-like bladders, while the granular cells were distributed at irregular intervals over the surface.

I have not as yet succeeded in the attempt to observe the young *Echinococci* in their earliest condition. A pig which was fed twice, at intervals of five weeks, with a large number of ripe *Tæniæ*, and was killed fourteen days after the last feeding, only exhibited worms similar to those which originated from the first feeding.[1] Some of them measured as much as 3 mm., the others varied from 1 mm. upwards, and even with the naked eye the above-described granular and radiate cells could be seen shining through. What was both new and striking to me was a thick border of granular spindle-cells, situated upon the now distinctly laminated cuticle, from which they could only with difficulty be separated. They agreed, however, with the adjoining granular cells, except in the difference of their form.

Besides the structures just described, the liver of the animal contained under the serous coating a number of small round or oval cysts (of 0·3 to 0·8 mm.). These I at first also regarded as *Echinococci*, especially since, like the latter, they belonged to the interlobular tissue, but I discovered to my surprise that instead of a parasite they enclosed a vegetable hair. This must have originated from the stomach, whose walls it had perforated, and afterwards penetrated into the liver. Apart from the analogy of this structure with the caterpillar-hairs found encapsuled in the mesentery and liver of the frog, this view was rendered more probable by the fact that the cysts were situated almost without exception on the concave surface of the liver. The comparison of these structures with the *Echinococcus*-cysts was of interest, since, not only were both bounded externally in the same manner by a layer of connective tissue, but enclosed the very same enveloping mass of granular cells.

[1] In the same organs as the above-described young bladders, Naunyn repeatedly found forms which perhaps represented the first stage of the bladder-worm. They were small round structures about four times the size of an embryo, and were composed of granular globules, and surrounded by a simple hyaline membrane. No embryonic hooks could be perceived.

Having been convinced by previous experiments that the *Echinococcus* possessed a far slower development than other bladder-worms, I determined to allow a longer time to a fourth animal, which had, however, like the former ones, been used meanwhile in other experiments (with *Tænia solium*, *T. marginata*, and *Trichina spiralis*). The examination was therefore not made until nineteen weeks after the feeding. I hoped that after this lapse of time I should find the *Echinococci* mature, and provided with heads; but this time also my hopes were doomed to disappointment. The experiment was certainly successful, in so far as the liver (and it alone) contained between thirty and forty bladders as large as nuts. On closer investigation these proved to be *Echinococci*, but in spite of their size they were in this case also still destitute of heads. Thus I had hitherto reared mere acephalocysts, of exactly the same nature as those which Kuhn has described with great accuracy in his above quoted monograph.[1]

In this case also most of these young encysted worms lay close under the serous covering of the liver, through which they shone more or less distinctly. Some had pushed out the covering before them into a lump, so that only the lower half was embedded in the substance of the liver. The adjacent parenchyma was of normal appearance, and not distinguished by abundance of blood, nor in any other way.

All the more surprising was it that the capsular wall of the parasite had in the meantime attained considerable thickness and firmness, such as I had never observed in any other bladder-worms of the same age. It was easily separable from the surrounding liver-substance, and the outer layers also could easily be peeled off it. At the same time its tension was so great that when cut it contracted powerfully, and this rendered it extremely difficult to extract the parasite without injuring its bladder. When this was successfully accomplished,[2] the worm appeared in the form of a transparent bladder of fluid, either round or nearly so; that is, of course, when the bladder was suspended in water. If placed on a firm surface it flattened out into a cushion-like shape, proving that the surrounding membrane possessed only a limited power of resistance. The average diameter amounted to something like 10 to 12 mm., but varied from 3 to 18 mm.

Here and there the otherwise transparent character of the bladder-worm was dimmed by a thin white margin, which was situated on the cuticle, and which, by the aid of the microscope, was recognisable as a portion of the layer of cells enveloping the connective-tissue cyst.

[1] *Mém. soc. hist. nat. Strassb.*, t. i., 1830.

[2] I recommend for this purpose dissecting under water—a method which has enabled me to extract *Echinococci* larger than the fist, uninjured from their capsules.

On closer observation, it was also seen that the surface of the *Echinococcus*-bladder was not smooth, but broken by numerous fine rents and cracks, which crossed each other and ran in different directions. The same phenomenon was afterwards observed in other *Echinococci*. It is as though the external layers, which are also the oldest, no longer being able to resist the increasing pressure of the growing mass, had ruptured. It is at least certain that the external cuticular layers are much more tightly strained than the inner ones. It is only necessary to cut the bladder at any point to get ocular demonstration of this fact by the immediate rolling up of the bladder-wall.

In bladders of about 1 cm. in diameter, on which our description is based, the general thickness of the cuticle was about 0·2 mm. On the internal surface the cuticle is more distinctly defined than on the external, and is laminated throughout its whole thickness. As has already been indicated, this lamination is obviously only the expression of a deposition in successive layers. While the external layers are gradually destroyed, new ones are continually being formed deep down, where the cuticle lies upon the parenchyma of the worm. These are seen chiefly in the form of a distinctly marked border, which extends along the boundary between the parenchyma and the cuticle, and sometimes even remains visible when the former of these is destroyed. The single layers of the cuticle are not, however, always marked off from each other with equal distinctness, nor always of the same thickness. As in the worms under consideration, the latter may be estimated on an average at about 0·0035 mm.

The parenchyma which extends under the cuticle is, in spite of its significance in the general life of the worm, of slight strength. It hardly ever measures more than 0·12 mm., and on a side view in fresh specimens is distinctly seen to be composed of two layers—an outer and an inner, as has already been mentioned in regard to the larger *Echinococci* from the second experiment.

The vesicular structures directed towards the internal cavity appeared, as in the *Cysticerci*, as rather sharply defined clear drops, with a somewhat fatty lustre, and not at all unlike the so-called "sarcode-drops." Most of them measured between 0·026 mm. and 0·036 mm., but there were some which were twice, or even three times larger. In the external layer the elements had much more emphatically the usual cellular character, although they were also pale, and not very distinctly defined. Their size was markedly smaller, being usually only about 0·07 mm., with the exception of the granular cells, which measured about twice as much. Between the cells there are found numerous coarse, strongly refracting grains, like

those above mentioned; and also distinct calcareous corpuscles of varying, and sometimes very considerable size. They are usually of a lenticular form, and agree in appearance (lamination and apparent formation of nuclei) with the corresponding structures of the related worms, although they differ from them in becoming pale on the application of acids, without evolution of gas. They are usually found singly, and are distributed over the whole surface of the worm.

Since we noticed in the other bladder-worms that the appearance of the first calcareous corpuscles was associated with the development of the excretory vascular system, it might be supposed that the *Echinococcus* also would be furnished with a similar apparatus. This supposition seemed all the more probable from the fact that, according to Naunyn's observation, the worms, even when of the size of a pea, exhibited a lively ciliary motion. The cilia were sometimes placed singly at some distance from each other, and at other times in groups of five to ten. They were not, however, situated on the parenchyma-layer itself, but, strange to say, on its inner surface, so that they projected freely into the interior of the bladder. At first they were only small, so that it was difficult to determine their form; but afterwards it was seen that at the lower end, by which they were attached to the cellular layer, they were spherically thickened, and thus probably always belonged to only one cell.

But in spite of this, neither Naunyn nor I have succeeded in proving the presence of a vascular system in this parasite. It is true that the cellular layer has, deep down, a peculiar system of net-like anastomosing cords of more or less considerable thickness (as much as 0·008 mm.), but these cords do not give one the impression of vessels. They appear rather to be solid bands of a homogeneous substance, and are, as Naunyn says, similar to those which are seen by the microscope on a glass smeared with fat or oil.

The ease with which they are destroyed renders the investigation of these structures specially difficult. One needs only to expose the worm for a short time to the influence of water or cold, or to press the preparation roughly, to witness the immediate shrivelling up of the former cords. Instead of the network, one finds in such cases large round drops of a sarcodic nature. Similar results are produced by the use of chromic acid and of Weissmann's solution of caustic potash (36 per cent.).

Since the network is not a vascular apparatus, it might perhaps be supposed to be contractile in function. But this interpretation is also inadmissible; not, however, because muscular fibres are altogether absent from the *Echinococcus*, as was before erroneously supposed, but because these muscular fibres, which one can hardly fail to see in the

larger bladders after staining, had neither in nature nor arrangement the slightest resemblance to that network. They appeared to be longitudinally extended, thin, sharply defined fibrils (0·001 mm. thick), which crossed in different directions, never uniting so as to form a closed layer or net, but always remaining separate, and at most turning aside from their former course at the points where they divide.

Whether this peculiar network has any connection with the ramified granular cells which I have already described in the larger *Echinococcus*-bladders from my second experiment, or is perhaps even formed from them, I must leave undecided, as also the question of its physiological significance. In this connection I can only remark that in one case, in which the still headless *Echinococci* measured from 12 to 20 mm., I sought in vain for the network, but again found the previously observed cells with ramified processes, and noticed that these were united here and there into real nets. It is true that the appearance of the network in the two cases was very different, and I must also own that the last-mentioned *Echinococci* were by no means in so good a state of preservation as the former ones. Not only was their parenchymal layer separated in some places from the cuticle, but they were without the drop-like bladders, which, in other specimens, lay upon the inner surface of the cellular layer, and in some places they even exhibited distinct holes, which could be readily observed on the cuticle.

When compared with the usual bladder-worms, the *Echinococcus* consequently exhibits a whole series of unexpected peculiarities. It is true that on the whole the analogy with the bladder of the *Cysticerci* is unmistakeable, but, on the other hand, the immense thickness of the cuticle, the absence of a powerful musculature, the slow growth, and the late development, not only of the tape-worm head but of the vascular system, and of the calcareous corpuscles (which, I may add, are only found in specimens of at least 8 mm. in diameter), present differences both numerous and important. Whether these peculiarities are mutually dependent on each other, and whether they have any connection with the thickness and firmness of the surrounding connective-tissue capsule, or with the well-known peculiar structure of the *Echinococcus*-head, we shall not further investigate. It is sufficient to indicate generally the possibility of such a connection.

In conclusion, I may remark that, in spite of its thickness, the cuticle of the *Echinococcus* possesses a very considerable capacity of imbibition. If the extracted bladder be placed in water or spirits of wine, it is observed that after a short time the parenchyma detaches itself more and more extensively, and ultimately becomes a bladder, suspended freely inside the cuticle, as has been depicted by Kuhn.

If a coloured fluid be used, such as solution of carmine, the space between the two bladders is immediately coloured, while the true interior remains for a time clear.

Structure and Development of the Echinococcus-Heads.

Von Siebold, "Burdach's Physiologie," Bd. ii., p. 183, 1837.

Huxley, "Anatomy and Development of Echinococcus veterinorum," *Proc. Zool. Soc.*, xx., p. 110, 1852.

Wagener, "Die Entwickelung der Cestoden," *Nova Acta Acad. Cæs. Leop.-Carol.*, Bd. xxiv. Suppl., p. 34, 1854.

Naunyn, "Entwickelung des Echinococcus," *Müller's Archiv f. Anat. u. Physiol.*, p. 612, 1862.

Rasmussen, "Bidrag til Kundskab om Echinococcernes Udvikling," *Vid. Meddel. nat. Foren. Kjöbenhavn*, p. 1, 1865.

The *Echinococcus* remains for a certain time in the condition which we have described, but after perhaps five months, and when it has become a bladder of 15 to 20 mm., it attains its full development by the formation of the heads, which bud forth in ever-increasing numbers from the parenchyma.

It is thus the presence of the head that characterises the adult *Echinococcus*, and that not of a single one or of a few, but of many thousands, all of which, so long as they live in their larval condition, remain in connection with the bladder-wall from which they originate and derive their nourishment.

In structure and mode of development these heads exhibit such numerous and important divergences from those of the other cystic bladder-worms, that it is necessary to examine them somewhat more closely.

As has been already mentioned, the *Echinococcus*-head in its adult state consists of a solid mass of cylindrical form, in which, besides the armed rostellum and the four suckers, there is an egg-shaped posterior portion, which sometimes passes by a broad base into the middle portion bearing the suckers, or at other times is separated from it by a constriction. The rounded end of this posterior portion, in which we recognise the neck of the future tape-worm, is furnished with a round depression, destined for the reception of the muscular stalk, by which the head is attached to its basis. Even after the detachment of the stalk, the depression is, for a long time, distinctly visible.

FIG. 322.—Head of *Echinococcus veterinorum.* (× 90.)

The length of the head (in its extended state) is at most 0·3 mm., and about the half of this belongs to the posterior portion, which is usually distinguished from the

anterior half by a more granular parenchyma (striated only in the interior), and by a greater accumulation of calcareous corpuscles. The calcareous corpuscles are somewhat large, or at any rate no smaller than in the other cystic bladder-worms, but their numbers are extremely variable in different specimens. On treatment with acids they exhibit a brisk fermentation.

In favourable objects one can distinguish four coiled longitudinal vessels, which unite in pairs before their entrance into the stalk, and are connected below the circlet of hooks by means of a ring-like anastomosis. Here and there are also some rapidly moving ciliated lappets. Otherwise the parenchyma of the body is upon the whole but little differentiated, and the musculature of the suckers in particular is much less distinctly defined than is usually the case in other cystic bladder-worms.

As to the hooks, it is well-known that they are distinguished from those of the adult *Tænia* (see Fig. 315) by the short and slender form of their roots, especially in the case of the larger ones. It sometimes appears as though the basal portion were wanting, as is indeed really the case (p. 582). This imperfect development of the roots affects the size of the hooks, as is shown by the fact that three linear measurements taken from hooks of the first order amounted to 0·03, 0·015, and 0·014 mm. respectively, and three taken from those of the second order 0·024, 0·013, and 0·014 mm. The first line extends from the point of the hook to the end of the posterior root, the second from the same point to the end of the anterior one, while the third indicates the distance between the ends of the two roots.

In spite of the solid nature of the head, the anterior half, with the circlet of hooks and suckers, may be entirely invaginated into the posterior portion. In this state the head has an almost spherical shape (0·18 mm.), like a *Vorticella*, with retracted circlet of cilia. In the middle of its free anterior border there is a more or less large depression, which marks the place where the invagination has taken place. Below this one sees the suckers, and further down, in the neighbourhood of the stalk, the circlet of hooks is observed shining through the parenchyma. The points of the hooks are, as a rule, directed upwards and outwards, so that, in its retracted state, the anterior part of the head has exactly the position and relation to the enclosing posterior portion, which we saw the *Cysticercus*-head to bear to its so-called "caudal bladder." Nevertheless it is impossible to regard the capsular envelope of the retracted *Echinococcus*-head as

FIG. 323.—*Echinococcus*-head, with the anterior part of the head invaginated. (× 90.)

a caudal bladder, and that not only because it forms an integral portion of the head, and is included in the body of the future tape-worm, but more especially because of its entirely different origin.

Before proceeding to the discussion of these conditions I must remind the reader that the earlier helminthologists believed the heads to be placed directly upon the inner wall of the *Echinococcus*-bladder. It was thought that they budded forth from this wall one after another, and remained attached to it for some time after they had completed their development. Even after the important discovery of v. Siebold, that these heads were enclosed in small special capsules situated upon the *Echinococcus*-wall, most zoologists remained to some extent at least true to their former opinion, inasmuch as they maintained that heads were formed and developed in two different ways. Von Siebold, for example, taught that some only of the heads originated in the interior of these capsules, and that others budded forth freely from the wall in the form of little processes, which, from the very first, were quite solid.

But further, it was even maintained, and indeed with the concurrence of all investigators, that the connection of the head with the tissue whence it sprang was only temporary. It was thought that after their development (and eventually by the rupture of the brood-capsules) the heads detached themselves from their origin, and, without losing their vital powers, roamed about freely for a long time in the fluid contained in the bladder.

FIG. 324.—Brood-capsule, with heads of *Echinococcus* in the interior. (×40.)

Unfortunately I am obliged to contradict most of these assertions.

Not only do the *Echinococcus*-heads originate, without exception, within the brood-capsules, discovered by v. Siebold, but also in their normal state these brood-capsules never rupture, nor allow the contained heads to escape. According to my observations, all parts of the *Echinococcus* (mother-bladder, brood-capsule, and head) *are throughout life in direct continuity* with each other, as indeed I have mentioned above.

I do not deny that one may often observe burst brood-capsules and isolated heads, but I have only observed these conditions in encysted worms, which were investigated some time after the death of their host. If the worms were fresh, I found, without exception, the conditions I have described: the heads all within their brood-capsules, and all of these attached to the inner wall by means of a small stalk.

But if the worm were exposed to the influence of external agents, or the parenchyma brought into contact with water, or any other diffusible fluid, the appearance altered, inasmuch as the brood-capsules burst, and the heads contained in them became free. The latter were either detached at once, or remained for a time in connection with the shrivelled and rolled-up wall of the capsule, and were united in groups, which were attached to the parenchymal layer by the stalk of the capsule, irresistibly reminding the observer of a colony of *Vorticellæ.*

FIG. 325.—Closed and ruptured brood-capsules, showing their connection with the parenchymal layer. (× 40.)

There can be no doubt that it is these phenomena of incipient or advanced maceration that have given rise to the numerous errors regarding the structure of the *Echinococcus*, and the mode of development of its heads, especially as the observations of Naunyn and Rasmussen have yielded results similar to my own.[1]

Regarding the genetic relations between the *Echinococcus*-heads and the brood-capsules, I must again differ from my predecessors. While they assert that the heads originate on the inner surface, and that they are from the first solid processes, I must, on the contrary, refer their origin to the outer wall, and maintain that, exactly as in the *Cysticerci*, the first rudiments of the heads are developed in the form of hollow buds.

The buds situated on the outer wall of the brood-capsules had already been occasionally observed, but they were generally mistaken, and regarded as adult heads, and on this ground many investigators (including Huxley) maintain that the outer surface of the brood-capsules is as well suited for the formation of heads as the inner.

The great susceptibility of the brood-capsules to the influence of reagents is explained by the thinness of their membrane, which even

[1] I must not, however, omit to mention that Klebs ("Handbuch der pathol. Anat.," Bd. ii., p. 586) has lately reported that in the human *Echinococcus* he has several times found isolated heads situated directly upon the parenchyma. Frerichs and Sommerbrodt are also said to have observed similar cases.

in the larger capsules hardly measures more than 0·004 mm. But in spite of this thinness the capsular membrane exhibits a distinct histological differentiation. In the interior may be perceived a delicate, sharply defined cuticle, which lines the cavity, and on the outside a thin layer of clear granular cells, which correspond to the superficial cell-elements of the true parenchyma of the *Echinococcus*, and differ little from it histologically. At the point of insertion of the head one can often distinguish a pair of vessels, which run thence into the capsular membrane. They anastomose freely with the vessels of the adjacent heads, and sometimes unite in the neighbourhood of the stalk of the brood-capsule into a true network, the offshoots of which are seen passing through the stalk to the parenchymal layer of the bladder-worm. In the latter they soon disappear from sight. At most, one can only follow them into the vessels of the stalk of an adjoining brood-capsule, with which they unite. On the *Echinococcus*-bladder itself, the vessels, if present at all, are much less distinctly marked than is the case in other bladder-worms.

I have never been able to find muscular fibres in the brood-capsules, although they not unfrequently exhibit a powerful peristaltic motion, which as a rule originates from the point of attachment. The drop-like bodies which lie on the inner surface of the cellular layer of the parenchyma are also wanting; but, in spite of this, I have no hesitation in regarding the brood-capsules as a local development of the bladder-wall. Since the separate layers have an exactly opposite position to those of the bladder-wall, they may be regarded in some respects as an invagination of the latter, just as we previously assumed (p. 357) when seeking to establish the morphological relation of the *Echinococcus* to the other bladder-worms.

As to the structure of the head itself, it is essentially the same as the head-process in the *Cysticercus*. First of all a discoidal thickening originates in the wall of the brood-capsule, which quickly rises and grows into a club-shaped process, whose longitudinal axis is perforated by a canal-like continuation of the interior of the brood-capsule. Like the cavity of the latter, the canal has on its inner surface a cuticle, and that a firmer one than was found there. Similarly, in spite of the resemblance in histological structure, the wall of the process is much thicker than that of the capsule.

Although composed only of cells, the rudimentary head has now a striking contractility. It stretches out, and may then contract to perhaps half its former length; it curves and swings like a pendulum to right and left, or may even be invaginated into the brood-capsule, so that the cuticle then becomes an outer coating, as in the *Echinococcus*-heads. This invagination sometimes occurs at an early stage, before

the rudimentary head has grown to any considerable size. Since one sometimes sees beside such small invaginated buds others which represent a later developmental stage, it often appears as though the *Echinococcus*-heads budded off as a whole inside the brood-capsule, and were developed from the first in their subsequent position with the cuticle outwards. At first a simple cylindrical process, the bud gradually assumes a club-like or pyriform shape, becoming constricted at its basal end. Afterwards it becomes modified by the formation of the hooks round about the free rounded end, where the border projects in a sort of circular fashion. Further back, at the bulging portion of the bud, the first traces of the suckers begin to appear (Fig. 327).

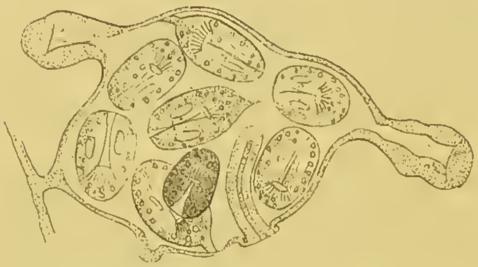


FIG. 326.—Brood-capsule of *Echinococcus veterinorum*, with adult and hollow rudimentary heads. (× 40.)

FIG. 327.—Development of the *Echinococcus*-heads from those hanging freely into the internal cavity of the brood-capsule (after Wagener). (× 90.)

The rudimentary hooks appear first in the form of a somewhat thick fringe of prickles, which surround the cephalic end like a girdle, but which afterwards all disappear except the foremost rows, which have grown gradually stronger. When the circlet of hooks has almost attained its subsequent structure, it is retracted along with the adjacent sucker-bearing portion, and sinks into the gradually enlarging posterior portion of the body. The internal cavity of the bud, which has not been lost by the invagination, then becomes obliterated, and the histological differentiation progresses, producing muscle-fibres, vessels, and calcareous corpuscles; and after constriction and the formation of a stalk at the point of insertion, the head has attained its final form.

I will not deny that the development of the *Echinococcus*-heads sometimes takes place in the way thus described (after Wagener). I have indeed sometimes observed *Echinococci* in which the rudimentary heads almost all projected into the brood-capsules, and exhibited the above developmental stages in uninterrupted succession. But I must most emphatically deny that the development of the heads in the above-described position is the only mode. Beside

the buds freely projecting inwards, one always finds others, and occasionally the majority, in which the head-rudiments hang from the brood-capsules into the common bladder-cavity, just like the head-processes of the *Cysticerci*. They undergo a metamorphosis just like the latter, and differ only in the fact that there is never a receptacular sac in which the head is bent together.

The analogy here referred to corroborates my opinion that the exogenous development of hollow buds is the typical mode of origin for the *Echinococcus*-heads, while the previously described endogenous mode, even if as frequent as Naunyn[1] and Rasmussen assert, is in reality exceptional. At any rate, these two observers agree in this—and this is the main point—that both modes of development occur in the *Echinococci*.

When the *Echinococcus* is developed, in the way last described, to that stage in which the histological differentiation begins, then its former attitude changes, and it becomes invaginated from the point of insertion into the internal cavity of the brood-capsule. What took place in the first mode at an earlier stage here occurs at a later stage, with the further difference that the invagination is usually restricted to the posterior (basal) half of the head. The inception of the hooked apparatus and of the suckers in such cases is thus no secondary state, but an occurrence which arises in the original formation, and is therefore to be regarded as typical. When the invagination of the basal half has taken place, then, as we have formerly described, the now contiguous walls of the hollow bud fuse with one another. The head solidifies and constricts at its point of insertion; in other words, it assumes the appearance of the endogenously developed head.

The older the brood-capsule becomes, the more does the number of the inmates increase, so that I have sometimes counted twelve to fifteen, and Eschricht twenty-two. Even in such populous capsules one often sees another new crop of buds (often three or four) at different stages of development. But not only do the heads of the *Echinococcus* gradually increase, but the number of the brood-capsules likewise, so that the larger and older worms sometimes contain many thousands.

[1] Naunyn notes (*loc. cit.*, p. 621, note) that in those *Echinococcus*-bladders which were warmed to about 35° C. before being opened, the buds were almost always found inside the brood-capsules, while in the same, after cooling, the buds were very frequently found on the outer surface. This would seem to show that the buds can be invaginated or evaginated according to circumstances—that the invagination is, in other words, by no means permanent. But this would, I think, also hold good on my theory; for why should the buds have the power of evagination and an internal cavity, if they develop from first inside the brood-capsule?

The formation and multiplication of these capsules takes place, according to my observations (confirmed by Naunyn), as follows:—

At distinct points on the parenchyma one notices at first small, wart-like elevations. These are proliferations of the cellular layer, which are even already (according to Naunyn) possessed of a number of actively vibrating cilia, which are still distinct at a later stage even after the formation of the head. When the elevations have grown to about double the thickness of the wall from which they spring, one can recognise inside them a small spheroidal cavity, which is very soon clad with a delicate cuticular membrane. Process and cavity then grow to perhaps three or four times their original diameter. The cellular layer, which had at first a considerable thickness, becomes thin, and forms at some point or other, usually opposite the point of insertion—the first hollow bud—which, sometimes as an external appendage (*C*), and sometimes inwardly invaginated (*D*), becomes the first head, which is soon succeeded by others.

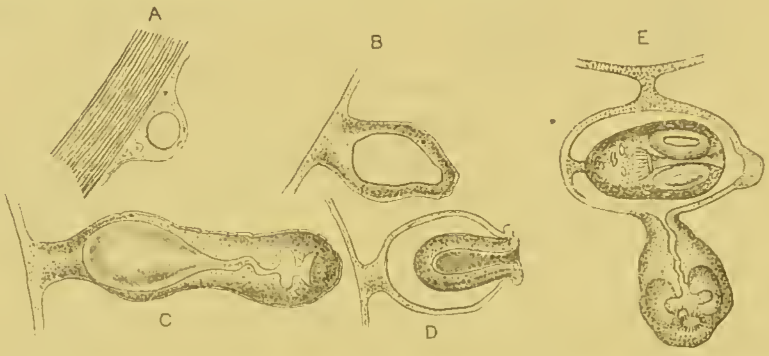


Fig. 328.—Development of brood-capsules (*A*) and of the appended heads. (*B*), first rudiment of the head; (*C*), further development; (*D*), invagination; (*E*), subsequent budding. (× 90.)

With the number of the budding heads the size of the brood-capsule also increases proportionally, so that many attain a diameter of 1·5 mm. Such large brood-capsules contain here and there perhaps a dead head, which is separated from its germinal layer, and is readily distinguished, by its shrivelled form and brownish colour, from the living and active, though but slightly mobile, heads.

It seems further as though the power of forming such brood-capsules were usually confined to certain portions of the *Echinococcus*-bladder, and never uniformly distributed over the whole inner surface. This is what we find in the *Cœnurus*, where the heads are budded off in groups here and there at varying distances apart.

There is considerable diversity as to the size which an *Echinococcus*-bladder must attain before it produces brood-capsules and heads. Usually this process may begin when the bladder has become as large

as a big hazel-nut. Under some circumstances it is postponed to a still later stage. In a cow which I examined, where lungs and liver were penetrated with perhaps 150 *Echinococci*, there were, besides the usual bladders thickly beset with brood-capsules, others which were still barren, although they had attained the size of a hen's egg, while in others, with a diameter of 10 mm., the formation of heads had already begun. In the so-called "*Echinococcus multilocularis*" the heads were sometimes found in bladders with a diameter of less than 1 mm.

We do not know how these differences are conditioned, nor how it comes about that certain *Echinococci* (the acephalocysts) never form brood-capsules or heads at all. One may indeed suppose that the nature of the parenchymal sheath is a determinant factor, but what the special peculiarities are is as yet unknown, and will probably remain unknown for long, owing to the difficulties which beset a thorough histological analysis of the bladder-wall.[1] This is also true in regard to the causes of sterility,[2] though disturbances of nutrition are probably largely influential in this connection.

The Formation of Daughter-Bladders and the different Forms of the Echinococcus.

Kuhn, "Recherches sur les Acéphalocystes :" Strassbourg, 1832.

Naunyn, "Entwickelung des Echinococcus," *Muller's Archiv f. Anat. u. Physiol.*, p. 612, 1862.

Rasmussen, "Bidrag til Kundskab om Echinococcernes Udvikling," *Vid. Meddel. nat. Foren. Kjöbenhavn*, p. 1, 1865.

With the above-described changes, the *Tænia echinococcus* has completed the bladder-worm stage of its development. The originally very small, six-hooked embryo has grown into a large bladder, which is beset internally with brood-capsules, which again produce an immense number of tape-worm heads.

What distinguishes the *Echinococcus* from other bladder-worms is not so much the great number of these heads, as the appearance of special brood-capsules, whose structure and development proves them to be structures as distinct as the bladder and head. They are related to the bladder, as the twigs of a tree are to the stem from which

[1] These difficulties explain the numerous erroneous hypotheses which interpret the parenchyma sheath even as a fat deposit, a simple epithelium, &c. But we need not point out that such views are inconsistent with any appreciation of the physiological importance of this layer, which represents neither more nor less than the whole of the active organic apparatus of the *Echinococcus*.

[2] Helm, "Ueber die Productivität und Sterilität der Echinococcusblasen," *Archiv f. pathol. Anat.*, Bd. lxxix., p. 141, 1880.

they bud forth. But as the twigs are morphologically nothing more than repetitions of the stem from which they spring, so are the brood-capsules, in a certain sense, nothing more than repetitions of the bladder which bears them. They are daughter-bladders, individually developed members of the *Echinococcus*, through whose budding the originally simple bladder-worm forms a colony. Although morphologically equivalent to the mother-bladder, they attain only an imperfect physiological individuality, as is so frequently the case in colonies. They remain connected with their mother-bladder, and undertake for the latter, according to the law of the division of labour, the function of head-formation. This specific function accounts for the differences which we have seen to obtain anatomically between the brood-capsules and the mother-bladders, and which essentially consists in the inverted order of the cuticle and the parenchymal sheath.

In many cases, especially in the *Echinococcus* of cattle (*E. veterinorum*), the worm remains in the above state till its host dies, or till the heads find an opportunity of becoming *Tæniæ* (p. 591). The only change, apart from the multiplication of brood-capsules and heads, consists in a continued, though perhaps but slow, growth of the bladder. We know, however, instances in which the *Echinococcus* (and that the simple form) has grown so as to attain a diameter of 15 cm. As a rule, indeed, the worm in this form attains but a comparatively small size—hardly greater than that of a fist or an orange.

In this increase in size the cuticle also participates, and that to a much greater and more striking extent than the parenchymal sheath. It becomes thicker the more the bladder-body grows, and in many cases measures as much as 1 mm. or more. The lamellar stratification remains as before, except that the lamellæ become more sharply defined, and increase in thickness. Nor does the elasticity of the cuticle experience any diminution: it seems in the large bladders hardly less conspicuous than in the small ones. One only needs to touch them to see how the tremulous motion spreads over the whole mass. This is not only perceptible to sight and feeling, but even to hearing, so that, after the example of Briançon and Piorry, the so-called "hydatid tremor" and rustling obtained on percussion have been used as a corroboratory diagnostic test.[1]

As the cuticle thickens, so does the connective-tissue cyst surrounding the worm. It becomes a sac, the wall of which often measures

[1] See on this point besides Piorry, "De la percussion médiate," p. 153, Paris, 1828, and especially Davaine, *Gazette méd.*, No. 20, 1862. Küchenmeister maintained for some time the erroneous opinion that this rustling noise was audible only in the hydatid form of *Echinococcus*.

5 mm., or even double that, and acquires a quite extraordinary firmness. It possesses its own arteries and veins, which spring from the neighbouring vessels, and are connected by a rich capillary network. On the smooth internal surface it bears at first a thin layer, which is fastened almost as firmly to the *Echinococcus*-membrane as to the surrounding wall of the cyst, and which, on microscopic investigation, is seen to be the cellular deposit already repeatedly mentioned.

As to the form of the *Echinococcus*, it is usually spherical (Fig. 317), but there are also bladders which possess an oval form, or by unequal development of the surface have become more or less bulging, as is to be seen in the adjoining representation. As a rule, such irregular forms find their explanation in the character of the connective-tissue cyst and its surroundings. They arise when the growing bladder encounters obstacles of varying strength.

FIG. 329.—Bulging *Echinococcus* in its natural size and position.

The fluid which fills the internal cavity of the *Echinococcus*-bladder has commonly a clear watery character. It is not coagulated either by boiling or by application of acids, and has in its fresh state no corpuscular contents. The brood-capsules and *Echinococcus*-heads, which the older observers saw swimming freely in this fluid, are in fresh specimens all attached to the internal surface. They shine through the body-parenchyma, which is usually transparent, though occasionally turbid at isolated spots, or even throughout.

The brood-capsules produced by these *Echinococci* have been already claimed as daughter-bladders, and, indeed, proliferating daughter-bladders. But they do not represent the only form of daughter-bladder which these worms can produce. Beside these, there not unfrequently appear other daughter-bladders, which possess exactly the structure and nature of an ordinary *Echinococcus*, yet do

not come to lie inside the bladder space, but are fixed on externally, as Kuhn long ago described in the case of his acephalocysts.[1]

In my earlier investigations I often saw this process of proliferation in cases of multiple *Echinococci*, and am still prepared to maintain the correctness of the observations. Naunyn has indeed urged a theoretical objection, which seems to me, however, as though directed rather against the form of my representation than against the actual facts.[2]

But before I enter into a discussion of the question, I must again expressly note that not all *Echinococci*, even in the above cases, exhibit this process, but only a few—generally those which are of a medium calibre. But since, as a rule, several daughter-bladders are thus formed at once, these are often found seated on the mother-bladder in groups attaining about the size of a pea.

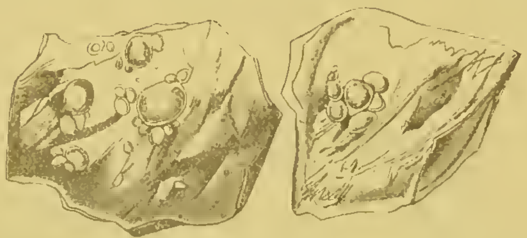


Fig. 330.—Proliferation of the membrane of an *Echinococcus* (nat. size).

The formation of daughter-bladders does not proceed directly from the external surface, but begins in the thick cuticle, and indeed in its deeper layers. At a definite point we notice at first, between the two lamellæ, a little heap of granular substance which presses the adjacent layers apart, and after some time becomes surrounded by a special cuticle. By repeated excretion of cuticular layers the granular heap becomes the centre of a special system of ever-increasing lamellæ.

It is not, however, only the formation of new envelopes which determines the growth of the embedded body, but also the increase in the mass of the contents, which gradually lose their former appearance, clear up, and pass through the changes which have been already described in treating of the development of the primary *Echinococcus*-bladders. At a certain developmental stage one finds the same stellate

1 Mégnin has lately observed a very remarkable case of this kind ("Sur une nouv. forme de ver vésicul.," *Journ. de l'Anat. et de la Physiol.*, p. 6, 1880). This was an *Echinococcus* which was developed in the leg of a horse, and had to a large extent penetrated and displaced its muscles. The *Echinococcus* of the upper part of the leg observed by Kanzow, and more closely examined by Virchow (*Archiv f. pathol. Anat.*, Bd. xxix., p. 180), ought also to be noted.

2 On the other hand, my observation has been confirmed by Pagenstecher (*Verhandl. nat.-med. Vereins, Heidelberg*, Bd. i., p. 5), and Rasmussen (*loc. cit.*), I have since observed that in 1857 Levison made the same observations ("Disquis. nonn. de Echinococcis," Dissert. inaug. Gryphiæ).

granular cells which we formerly noted. There can hardly be any doubt, then, that these embedded bodies are rightly regarded as daughter-bladders.

They gradually emerge of course from the deeper parts of the cuticle, since new cuticular layers are always arising internally, as those outside (p. 600) gradually disappear. The superjacent layer of the cuticle of the mother-bladder becomes pushed forward as a sort of hernia. The more the daughter-cell grows, the more accentuated does the protrusion become, until it finally bursts and sets free its inmate. In many cases the daughter-bladder becomes abortive soon after its isolation (perhaps under the pressure of the surrounding wall of the cyst), but in other cases it develops beside the mother-bladder. It is at first enclosed in a lateral pouch of the original cyst, but in the course of time it usually acquires an independent envelope, a partition wall gradually growing up in the space intermediate between the mother and daughter-bladder. In the last stage it is of course hardly possible to distinguish the secondary *Echinococcus*-bladders arising by proliferation from the primary parasite, which originated from the metamorphosis of a six-hooked embryo. A valid difference, however, seems to me to lie in the fact that the daughter-bladders are able to produce brood-capsules sooner than their mothers.[1]

The objections which Naunyn urges against my observations have to do less with the real facts—for he himself admits having seen peripheral daughter-bladders—than with my assertion that they arise "independently of the parenchymal layer of the mother." In this expression I have, indeed, affirmed too much,—more, in fact, than I intended. At first I only wished to indicate that the daughter-bladders have an independent development, and exhibit no permanent connection with the parenchyma of the mother. As to the nature of the granular mass which furnishes the point of origin of the daughter-bladder, no additional light has been cast upon it by my observations, but I have no scruple in deducing it from the parenchymal layer of the mother. It obviously represents a portion of the latter, a bud-like outgrowth, so to speak, which separates itself from the matrix,[2] and becomes ever further separated from it by the subsequently formed cuticular layers. In agreement with this is the fact that the daughter-bladders, so long as they are small, lie in the deeper layers of the cuticle, and only gradually work their way outwards.

[1] Morin observed the formation of heads (in a case of *Echinococcus multilocularis*) in the daughter-bladders, although none of them had become separated ("Deux cas de tumeurs à echinocoques multiloc.," Dissert. inaug. Lausanne, p. 32, 1876).

[2] Naunyn sometimes saw (*loc. cit.*, p. 631) a very fine canal running through the subjacent layers of such a peripheral daughter-bladder, and even opening into the latter, so that it looks as though this separation were sometimes delayed to a later period.

The form of *Echinococcus* whose proliferation I have here described is that which Küchenmeister formerly maintained to be the representative of a distinct species—*E. scolecipariens.* The name is not very distinctive, since the other forms of *Echinococcus* also produce scoleces. It might have been more appositely called *E. granulosus* or *simplex,* if one do not prefer Kuhn's designation of "exogenous" *Echinococcus.* After our previous discussion, we need not repeat that it does not represent any distinct species.

This simple *Echinococcus* is specially frequent in domestic mammals, particularly in the pig, which, in this country, is the animal most infested with *Echinococcus.* But even in man it is not a rarity. Küchenmeister, in the first edition of his "Parasiten," recounts, it is true, only two cases—one observed by Gescheid (*Echinococcus* of the eye), and another by Eschricht (*Echinococcus* in the liver, from Iceland, usually compound); but a very superficial review of the numerous cases of *Echinococcus* now reported is sufficient greatly to increase the number.[1] The case of Eschricht is further of importance, inasmuch as he was one of the first expressly to mention the head in the simple *Echinococcus* occurring in man.

Generally the *Echinococcus granulosus* occurs in the omentum under the peritoneal covering of the abdominal wall and in the bones, but there are also instances of its occurrence in other organs, especially the liver, spleen, lungs, which attract our attention all the more readily since the worm in these places usually grows to a considerable size. We must, therefore, note expressly that the simple *Echinococcus* is not the only form which the above organs harbour; indeed, another form is very frequently found, which is characterised by the possession of daughter-bladders internally. In the lungs and liver this compound *Echinococcus* is actually much more frequent than is the simple one, which does not, of course, exclude the possibility of their occasional occurrence together in the same body, and often close beside one another.[2]

This second compound form of *Echinococcus* is that which Küchenmeister designated *E. altricipariens,* a name which has now fallen into disuse, and may very suitably be replaced by the name *E. hydatidosus* (*Echinococcus endogena* of Kuhn).

This *Echinococcus hydatidosus* is distinguished from the above-

[1] Sommerbrodt, who has collected the cases of *E. granulosus* occurring in man (*Archiv f. pathol. Anat.,* Bd. xxxvi., p. 272), estimates them at seventeen, but this number has been tripled by Böcker, Neisser, and Helm.

[2] Specially instructive is a case observed by Haen (quoted by Davaine, *loc. cit.,* p. 367), where simple and hydatiform *Echinococcus*-bladders occurred in the liver of the same individual. Similar cases are also reported by Wunderlich (*Archiv f. physiol. Heilkunde,* p. 283, 1858), by Davaine (*Mém. Soc. biol.,* p. 106, 1857), and by Helm (*loc. cit.,* p. 148).

described simple *E. granulosus,* not exactly by the presence of daughter-bladders—for these may be produced also by the latter—but by the presence of daughter-bladders in the interior of the mother-bladder, structures which are not only found often in large numbers, but which may grow to an appreciable volume, and sometimes themselves produce daughter-bladders. Further, the large size which the hydatidose *Echinococcus* usually attains is also noteworthy; cases are known in which it weighed from 10 to 15 kilogrammes, and therefore far exceeded the largest *E. granulosus.*

I cannot conceal that, among the almost countless cases of *E. hydatidosus* reported in medical literature, there are many in which no mention is made of the mother-bladder, so that the bladders (hydatids) lay apparently immediately in the surrounding connective-tissue cyst, and were in fact to be regarded as daughter-bladders in the same sense as those of *E. granulosus.* This silence does not, of course, warrant us in inferring the actual absence of the common mother-bladder—not only because the descriptions often suggest that the mother-bladder was attached to the enveloping connective-tissue cyst, and was considered to be an integral part of the latter, but also because it not unfrequently happens in the course of time that the mother-bladder is destroyed by the continually increasing number of daughter-bladders. Böcker and Helm recount a whole series of cases in which the mother-bladder had either degenerated or been torn, and here and there the membranous remains were still found in the pulpy mass enveloping the daughter-bladders.

In regard further to the co-existence of daughter-bladders and heads, the above reports must be received with caution. This is especially true of the oft-repeated assertion that *E. hydatidosus* is devoid of heads—an assertion which was explained by Davaine, who supposed that the formation of the daughter-bladders preceded by some time the formation of heads.[1] The commonly asserted absence of heads shows only that the observers failed to find them. And this may all the more readily occur, since the daughter-bladders of the hydatidose *Echinococcus* are, in point of fact, often sterile. I had to examine many daughter-bladders before I found those with brood-capsules and heads. Other investigators, such as Lebert and Helm, have had a similar experience. On the other hand, there are hydatidose *Echinococci* whose bladders all bear heads. Thus Eschricht reports that in one of his cases all the daughter-bladders, some thirty in number, both large and small, from the size of a hen's egg to that of a pea, contained brood-capsules and heads. Helm similarly reports

[1] "Rech. sur les hydatides, les échinococques et le cœnurus," *Mém. Soc. biol.*, 1855; *Gaz. Méd.*, 1852.

that in many cases he found the mother-bladder beset with brood-capsules and heads sometimes by itself, and sometimes along with the daughter-bladders. Where the proliferating and sterile bladders occur together, the former are sometimes (Levison, Helm) characterised by a more transparent nature.

As to the age, or perhaps more correctly the size, of the *Echinococcus* associated with the appearance of the daughter-bladders, only an uncertain answer can be given. So far as I know, there is no authentic case in which an *Echinococcus* smaller than a walnut contained hydatids, which casts doubt on Davaine's statement mentioned above. But that the production of daughter-bladders does not exclude the formation of heads, is evident enough from the fact that along with the latter one often sees bladders of all possible sizes, from that of an apple to that of a pin-head, with all intermediate stages.

This continued proliferation explains also the large size of the daughter-bladders, which is observable in many cases of hydatidose *Echinococcus.* We know instances where the number might have been estimated at thousands.[1] Most of these reports, however, are of somewhat early date, and we are somewhat inclined to place them in the same category as the reports of tape-worms 800 yards long. I myself, I must confess, belonged to the ranks of these sceptics, until, through Professor Luschka, I became acquainted with a case not a whit inferior to any of these older reports.

The case was that of a woman sixty years of age, who for several decades had suffered from a tumour which was for a while considered as an extra-uterine fœtus, until its increasing size and the absence of distinct confirmatory symptoms led to the abandonment of this diagnosis. On *post mortem* examination the tumour was seen to be a huge *Echinococcus*, which originated in the liver, and had gradually grown to become a sac weighing thirty pounds. Within it there was an immense number of daughter-bladders, some thousands at least, varying from the size of a fist to that of a pea and less, but neither heads nor hooks could be found.

Echinococci with some hundred bladders are more frequent, but as a rule the number remains below this, and is often about 25-50. These differences depend partly, but not wholly nor exclusively, on the age of the *Echinococcus.* In an *Echinococcus* weighing from eight to

[1] Besides the cases collected by Davaine (*loc. cit.*, p. 365), in which the number in some cases amounts to 9000 (!), I may also note Russell (*Dubl. Journ. Med. Sci.*, vol. xii., No. 35, 1837), and Knaffl (*Oesterr. med. Jahrb.*, Bd. xx., Stück 3; *Schmidt's Jahrb.*, xxviii., No. 10), where two cases of "several thousands" are reported. Even in the domestic animals such cases occur. My uncle, F. S. Leuckart, once saw a fat pig whose abdominal cavity was filled with "several thousand hydatids," which originated from a recently ruptured *Echinococcus* in the liver, which it had almost entirely destroyed.

ten pounds taken by Leroux from the liver, there were hundreds of daughter-bladders which varied between the size of a pea and that of an egg;[1] while an *Echinococcus* weighing fifteen pounds, observed in the thoracic cavity by my now deceased friend Krüger in Brunswick, contained only twenty-five bladders, and an *Echinococcus* of 12 pounds found by Lelouis in the Douglas' pouch of a man contained only ten about the size of nuts.[2]

The number of enclosed daughter-bladders may indeed sink still further, as is proved by two cases mentioned by Krabbe and by Andral, in which two large *Echinococci*, occupying the whole lower lobe of the lungs, enclosed in the one case two, and in the other three small daughter-bladders. The number may, on the other hand, greatly increase even at an early stage, as is proved, *e.g.*, by a case observed by Velpeau, in which an *Echinococcus* about the size of an egg, which had developed under the shoulder-blade,[3] on being punctured set free at least a hundred bladders, of which the largest were about the size of a hazel-nut, and the smallest hardly larger than a pin-head.

From these instances one cannot but be convinced that the vegetative relations of the *Echinococcus* present great divergences, of which the determinant factors are not yet clearly known. All the more must we avoid forming judgments on the strength of presupposed standards.

If the daughter-bladders be but few in number, so that they can develop unhampered on all sides, then they have always a beautiful and regular spherical form. In other cases the mutual pressure produces the most manifold shapes. Some are more or less compressed, others constricted like a sand-glass, while others again exhibit three, four, or more smaller flattenings. In spite of all differences of appearance, these agree histologically with the simple *Echinococci*, as I need hardly repeat after what has been said above.

The question readily suggests itself, *How do these daughter-bladders arise?* The answer is not so readily obtained. From the fact that the so-called "secondary hydatids" are in their properties as thoroughly identical with the mother-bladder as are the exogenously produced daughter-bladders, one might reasonably suppose that they originated in the same way, in other words, that they were developed from small beginnings in the wall of the mother-bladder. Only this difference would obtain between them, that in the simple *Echinococcus* the daughter-bladders emerge on the exterior, while in the hydatid form they appear and remain within the cavity of the mother-bladder. This is in fact Kuhn's opinion, and was also mine in the first edition

[1] Davaine, *loc. cit.*, p. 456. [2] *Ibid.*, p. 513. [3] *Ibid.*, p. 544.

of this work. I have now, however, come to a different conclusion. For although the formation of peripheral daughter-bladders is to be observed in the hydatidose *Echinococcus*, this takes place only in connection with the multiplication of the hydatids, while they originate by a different mode, namely, the heads and brood-capsules (which we have shown to be morphologically equivalent to the bladders), undergo a retrograde metamorphosis, in consequence of which they assume the form and structure of daughter-bladders.

Bremser, v. Siebold, and Wagener had previously asserted such a transformation in regard to the head, and Eschricht in regard to the brood-capsules, but, the detailed proof being wanting, their statements did not meet with the consideration which they deserved. But this gap has been filled up by the publications of Naunyn and Rasmussen, and the origin of the organs in question has been sufficiently established. I must add, however, that Rasmussen differs to some extent from Naunyn, inasmuch as he maintains that only the brood-capsules wander about in the daughter-bladders, and denies that the heads have this capability. But according to my own observations he is mistaken on this point. In the *Echinococcus* of the sheep, I have observed that the processes referred to by Naunyn may occur exactly as he has described. In the *Echinococci* of this animal the occurrence of secondary hydatids is by no means so rare as is generally supposed. Naunyn also made his investigations principally on the *Echinococcus* of the sheep, but was at the same time convinced that in the human *Echinococcus* the hydatids originate in exactly the same way.

Among the countless heads which are found in the larger *Echinococcus*-bladders, partly in the interior of the brood-capsules, and partly free in the fluid of the bladder, one not unfrequently notices some which are modified in a peculiar manner. They are more transparent and larger than the others, and in the inflated hinder part of the body contain a cavity filled with a clear fluid, through which a distinctly fibrous band, which not unfrequently encloses vessels, runs towards the heads. The character of this cord seems to favour the supposition that it has originated by separation from the middle layer. On the inner surface of the body-wall, which accordingly ought to correspond to the peripheral layer of the body, are seen the ciliary lappets previously

FIG. 331.—Metamorphosis of an *Echinococcus*-head into a bladder in the interior of the brood-capsule. After Naunyn. (× 60.)

discussed, and also a network of fine threads, which proceeds from the more compact anterior end, and exhibits several distended portions enclosing fatty drop-like structures of various size. The outer covering is formed of a structureless cuticle, which becomes thicker with the increasing size and roundness of the body, and exhibits a lamination which becomes more and more distinct.

Gradually the internal cavity passes from the posterior to the anterior body. The suckers disappear, the calcareous corpuscles are dissolved, and the parenchyma of the head, and the network which we have mentioned, spread themselves equally over the wall of the body in the form of a fine cellular layer. The circlet of hooks alone reveals the origin of the bladder. But this also disappears when the bladder is about the size of a millet seed, and then the former head does not differ in a single point from a young *Echinococcus*-bladder.

In cases where the modification of the heads begins in the interior of the brood-capsule (Fig. 331), the latter bursts before the metamorphosis of the head is completed, so that the young hydatids are all found free within the bladder.

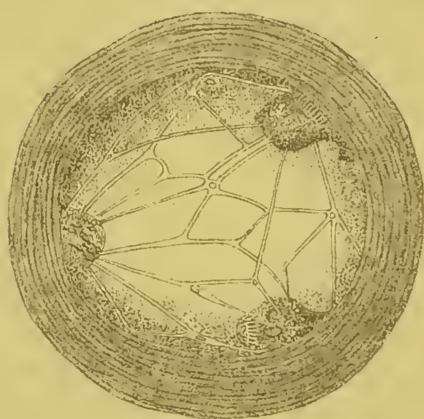


FIG. 332.—Metamorphosis of the brood-capsules into bladders. After Naunyn. (× 90.)

But it is not only the heads that undergo this metamorphosis, but under some circumstances also the brood-capsules, and especially, it would seem, those which have already lost some of their heads. The transformation begins with a thickening of the hyaline membrane. When this has proceeded so far that the latter possesses the nature and lamination of a firm cuticle, the bladder is set free from its basis. The superficial parenchyma disappears, but in place of it a new one orginates in the interior, formed from the substance of the heads, which apply themselves to the cuticle, gradually lose their form, and ultimately become a boundary layer, which is equally distributed over the internal surface. The circlets of hooks, which may at first be perceived in the interior, leave no doubt as to the origin of this inner layer. But afterwards, when these have been destroyed and have disappeared, it is impossible to find any indication of its origin. The bladder then resembles a young *Echinococcus*, and all the more closely, since the parenchyma again exhibits that reticular marking which we have already often noticed in these bladder-worms.

In some cases this metamorphosis is somewhat modified, inasmuch

as it affects not the whole brood-capsule, but only a certain part of it, which is then at an early stage marked off from the rest by a constriction.

According to Rasmussen, however, the laminated cuticle of the secondary hydatids does not originate by the thickening of the hyaline inner membrane, but upon the external surface of the brood-capsule, which from the first is covered by a delicate cuticular layer. The metamorphosis of the brood-capsules into hydatids would accordingly be a kind of encapsulation, as was indeed previously asserted by Eschricht. Any change of the parenchymal sheath would thus be unnecessary, and its formation would be independent of the destruction of the heads, which in its turn would be a process of only subordinate importance.

When once they have arisen, the secondary hydatids are also able to multiply by external buds, and that in the very same way as we have described in the simple *Echinococcus*. The investigations of Davaine, as well as those of Levison and Rasmussen, leave no doubt regarding this point. The latter saw the proliferation even in hydatids which hardly measured half a millimetre, while Davaine observed it in older and larger daughter-bladders.

It has already been mentioned that the secondary hydatids also correspond to the simple *Echinococcus*-bladders, as regards the production of brood-capsules and heads. By this vesicular metamorphosis these bladders can of course again produce hydatids in their interior, so that three generations are then enclosed one within the other. Even in sterile hydatids one sometimes finds granddaughter-bladders, but it would seem that these owe their origin to no new formation, but to certain heads which undergo their vesicular metamorphosis at the same time as the enveloping germ-capsules, and without leaving them. Naunyn mentions that he has often found such heads in the interior of small hydatids which had been newly formed from brood-capsules.

If, however, the secondary hydatids all originated in the way which we have described, as the results of the metamorphosis of the heads and germ-capsules (and against this view there are no *à priori* considerations, since both structures are morphologically perfectly equivalent[1] to the bladder), then there could of course be no sterile *Echinococci* with daughter-bladders in their interior. The *Echinococcus*

[1] I may take this opportunity of mentioning that very often structures of the same morphological value undergo a subsequent transformation. We know, for example, that in crabs the swimming legs are transformed in the course of the metamorphosis into mouth-appendages, and are functionally replaced by others subsequently formed. We also know that the nutritive polyps of certain Tubularidæ modify their former structure from external and internal causes, and change into proliferating individuals (Blastostyles).

hydatidosus would thus always be capable of producing brood-capsules and heads as well as daughter-bladders.

It is nevertheless equally certain, from the investigations of Helm, which, being specially directed to this point, admit of no doubt that there are hydatid *Echinococci* which are completely destitute of heads.[1] In order to reconcile these forms with the above view, we must suppose either that the worms had in the course of time lost the capability of producing heads, or that the brood-capsules had become daughter-bladders before the differentiation of the heads.

The possibility of these processes cannot be denied, but Naunyn has in the meantime proved that under some circumstances the secondary hydatids originate directly, and independently of the other products of proliferation.

The process exhibited in this alternative mode of formation consists essentially in the sacculation of the *Echinococcus*-wall. This begins by the collapse of the bladder after the partial loss of its fluid, so that surfaces formerly opposite are here and there brought into contact. When this contact, as often happens, leads to coalescence, a portion of the parenchymal sheath separates like a fold from the rest of the covering of the *Echinococcus*-bladder, and the portion of the parenchyma thus separated forms the starting-point of the new formation. First of all, it is changed by flattening and disappearance of the internal cavity into a band, which in its turn generally breaks up after a short time into a number of pieces. These become surrounded by a system of concentric cuticular lamellæ, and becoming hollow inside, form so many new hydatids. The process bears the greatest resemblance to the above-described exogenous budding, except that when the hydatids grow out of the enveloping fold and fall off, they do not make their way outwards, but into the bladder-space.[2]

In some cases the process which we have described is only imperfect, and then there arise forms in which the inner surface of the cuticle (as both Eschricht and I observed) is covered with cauliflower-like excrescences, which always enclose hollow spaces.

The two forms of *Echinococcus* which we have hitherto been considering, *E. granulosus* and *E. hydatidosus*, however different they may be in other respects, agree at least in this, that they both form bladders of considerable size. We know, for example, that they sometimes

[1] *Loc cit.;* regarding this point, see especially Observations iv., ix., and xi.

[2] Thus I was by no means wrong when I formerly sought, in the first edition of this work, to derive the daughter-bladders of the *Echinococcus hydatidosus* from peripheral buds, which essentially differ from the buds of the *E. granulosus*, only in reaching the interior of the mother bladder by separation. I only erred in regarding this mode of origin as the only one that ever occurs.

grow as large as or even larger than a child's head, which is, however, more frequently true of the *Echinococcus hydatidosus* than of the other.

A third form of *Echinococcus* (*E. multilocularis*) differs from these principally (apart from the first stages of development, which have not yet been observed) in being composed not of a simple bladder, but of a group of small, even very small, bladders, which lie in considerable numbers near each other embedded in a common soft stroma.

We find this *Echinococcus multilocularis* almost exclusively in man,[1] and indeed with few exceptions in the liver,[2] in which, along with the stroma, it forms a usually somewhat round, firm body, about the size of a fist or even of a child's head, and having at first sight more resemblance to a neoplastic growth than to an animal parasite.

If a section be made through the tumour, numerous small cavities are found in the interior, usually of irregular form, separated from each other by a more or less thick connective-tissue mass, and with somewhat transparent gelatinous contents. In the intervening mass there is seen here and there a blood-vessel or a collapsed bile-duct. As far as the tumour extends, the proper substance of the liver has completely disappeared, so that the limits of the former are distinctly defined, and its extraction presents no great difficulties. But occasionally there may be seen issuing from the tumour a number of white, pearly moniliform cords, and even thicker off-shoots, which make their way into the adjoining liver-parenchyma, and become new foci of *Echinococcus*-formation at some distance from the tumour.

Fig. 333.—Section through an *Echinococcus multilocularis* (nat. size).

The alveolar structure of the tumour and the associated gelatinous bladders remind one so forcibly of certain colloid growths, that it is easy to understand

[1] More recently, however, it has also been observed in the ox, for example by Huber (*Jahresber. d. naturhist. Vereins in Augsburg*, 1861), Perroncito ("Degli Echinococci negli animali domestici," p. 69, Torino, 1871), Harms (*Jahresber. d. k. Thierarzneischule in Hannover*, iv., p. 62, 1872), and Bollinger (*Deutsche Zeitschr. für Thiermedicin*, Bd. ii., p. 199, 1875). In Huber's case, there were, beside the *E. multilocularis*, an *E. hydatidosus* as large as a fist, and a number of simple *Echinococci* (with heads)—thus a collection of all the forms which are known to us.

[2] Among the cases with which we are acquainted (about forty) there is only one in which the *E. multilocularis* was certainly observed outside the liver, namely, in the supra-renal body (Huber, *Deutsches Archiv f. klin. Med.*, Bd. iv., p. 613). It is true that the

that the earlier observers never thought of doubting their pseudo-plastic nature. And they must have been confirmed in this erroneous opinion by the circumstance that the multilocular *Echinococcus* has a peculiar tendency to central ulceration (originating at first in the stroma), which generally causes the death of the host. Even the observation of Zeller,[1] that the gelatinous bladders of the alveoli occasionally contained a brood of *Echinococcus*-heads, did not avail to alter the prevailing opinion regarding the so-called "alveolar colloid" of the liver. The presence of these animals was regarded as an accidental complication, and the pseudo-plastic nature of the growth was never doubted until Virchow ultimately established the complete correspondence of the so-called "colloid masses" with small *Echinococcus*-bladders.[2]

Virchow's discovery removed all doubt on this point. The only question was whether or not the individual *Echinococcus*-bladders of the tumours originated independently of each other; in other words whether they owed their origin to an extensive, perhaps often repeated, immigration of *Echinococcus* embryos, or were produced by continuous budding from one, or perhaps a few mother-bladders. The latter view seemed the more probable, and all the more since the early observers had frequently noted the irregular form and numerous club-shaped processes of the colloid *Echinococcus*-bladders.

Virchow was therefore entirely in the right when he sought to explain the form of the multilocular *Echinococcus* by the supposition of a repeated external proliferation. It is more doubtful whether he was equally right in supposing this peculiar form to be due to the fact that the multilocular *Echinococcus* had taken up its abode in the lymphatic vessels. At present, perhaps as much can be urged against this conjecture as can be adduced in favour of it. Even if we suppose that the root-like processes of the tumour (frequently observed, and especially in Virchow's case) follow the course of the lymphatic vessels, the primary position of the *Echinococcus* would be by no means determined, since it is quite well known that the growing *Echinococcus* not unfrequently seeks out the most diverse paths, and penetrates with special preference into adjoining cavities, that is to say, into the blood-vessels, and in the liver also into the gall-ducts. Indeed, we have gradually become convinced that the multilocular *Echinococcus* may be found on different occasions in all these cavities.

lungs (Lebert), the pulmonary artery, and the sub-peritoneal tissue of the uterus (Scheuthauer), and even the intestinal wall itself, are mentioned as the seat of *E. multilocularis*, but all these statements are doubtful, since there is some suspicion that they refer to multiple *Echinococci*.

[1] "Das Alveolarcolloid der Leber:" Tübingen, 1854.

[2] *Verhandl. der Würzburger phys.-med. Gesellsch.*, Bd. vi., 1856.

Our knowledge of the primary position of the *Echinococcus* is upon the whole so scanty, that we are far from being able to utilise the differences in its occurrence for the explanation of the different forms of *Echinococcus*. In pigs the *Echinococcus* of the liver lies, as we have already mentioned, originally in the interlobular spaces; but whether in the lymphatics, bile-ducts, or blood-vessels, which together form this capillary network, cannot be determined. For my own part, I am most inclined to place the primary seat of the *Echinococcus* in the blood-vessels, and I can at least urge in favour of this opinion the analogy of *Cysticercus pisiformis* and *C. tenuicollis*, and perhaps also the wide distribution of the *Echinococcus* itself. Virchow, on the contrary, thinks that the multilocular *Echinococcus* develops in the lymphatics, while Schröder van der Kolk,[1] Friedreich, and Morin are convinced that it really originates in the gall-ducts.

My own acquaintance with the multilocular *Echinococcus* is based on the investigation of some preserved specimens. Not only had Professor Luschka the kindness to place at my disposal portions of two tumours investigated by von Zeller and himself,[2] but I was also so fortunate as to find an entire (though of course extracted) tumour in v. Sömmering's collection, which now belongs to the Giessen University Museum.[3] The latter, which is about the size of a duck's egg, is flattened at one end, and has there a cavity of the size of a nut, with walls irregularly eroded. This cavity unquestionably represents the ulcerated cavity found quite constantly in specimens of *Echinococcus multilocularis* at a certain stage of development. As may be seen from the above description, the *Echinococcus*-bladders are on an average larger than in the two other cases known to me, but otherwise they perfectly correspond with them.

The nature of the material at my disposal has rendered it impossible for me to add anything new to the earlier observations, and particularly to the statements of Zeller and Virchow. Thus all that I can offer hardly amounts to anything more than a confirmation of what is already known. More recent observations[4] have in fact done but little to advance our knowledge of the *Echinococcus multilocularis*.

The size of the cavities, and of the *Echinococcus*-bladders which

[1] Ruyssenaers, "De nephritidis et lithogenesis quibusdam momentis," Dissert. inaug., Traj. ad Rhen., p. 49, 1844 (cited by Virchow).

[2] See *Virchow's Archiv f. pathol. Anat.*, Bd. x., p. 206.

[3] In the catalogue of this collection, numbered 215, with the note—"Tumor hepatis viri, similis Baillie Fasc. v., Pl. iii., Fig. 3."

[4] See especially the statements of Friedreich (*Archiv f. pathol. Anat.*, Bd. xxxiii., 1865), of Klebs (*Handb. d. pathol. Anat.*, Bd. ii., p. 511, 1869), and of Marie Prougeansky, ("Ueber die multiloculäre ulcerirende Echinococcusgeschwulst in der Leber," Inaugural-Dissert., Zurich, 1873), and Morin (*loc. cit.*).

fill them, usually varies in such a manner that the largest cavities, which sometimes have a diameter of 3 or 4 mm., are found in the middle of the swelling. But between them are much smaller bladders, and towards the periphery these gradually become more abundant, bladders of less than 0·1 mm. being not unfrequently found.

All the bladders, even the smallest, exhibit the well-known structure of the *Echinococcus*-bladder. They possess a laminated, transparent cuticle of great elasticity and considerable thickness, which, in the larger bladders, measures 0·08 mm. or even more, but in the smaller ones sometimes only 0·01 mm. Occasionally one finds bladders, even among the larger ones, with still thinner walls, so that here, too, the same variations are observed which we noticed in the newly developed *Echinococci*. As in the latter, the interior of the bladders is at first filled with a molecular mass, whose coarser granules exhibit a distinctly fatty lustre. As soon as the bladder grows the central space becomes clear, and the former granular contents appear in the form of a membranous lining of the cuticle, with more or less large and abundant calcareous corpuscles. In the parenchymal layer of the larger bladders, Virchow very "frequently observed a large-meshed network of anastomosing, stellate structures, somewhat swollen at the nodes, and extremely fine in the connecting threads, which, being embedded in the hyaline, structureless, intervening substance, presented the greatest resemblance to the stellate cells of the gelatinous tissue. In some places the cells were larger, their processes and connective threads broader and canal-like, their bodies larger (some even 0·2 mm. long and 0·1 mm. broad), and with a more distinct granular deposit. They had thus a very striking resemblance to lymphatics in the course of development." There can be no doubt that the structure thus described by Virchow, and afterwards in a similar manner by Friedreich, is identical with that which I observed in the large, still headless *Echinococcus*-bladders.

But in the great majority of the bladders of this *Echinococcus* the heads are never developed. In the foregoing cases I examined many, both large and small, before finding a head, and such has been the experience of earlier and more recent investigators, while many have sought them quite in vain. In my observations the bladders which contained the heads were usually of medium size—perhaps 2 mm. or more—but the heads were always either isolated or in groups of three or four. In size and form the hooks (36-42 in number) exhibited no differences from those of the usual human *Echinococci*.

Under some circumstances, however, the multilocular *Echinococcus* attains a considerable fertility. So was it at least in a case from the Zürich Hospital investigated by Marie Prougeansky, in which half

the bladders, both large and small, were provided with heads, so that in single preparations one could count more than thirty. The smallest bladders usually contained only one head, which almost filled the whole interior; but others contained several, which were sometimes of normal structure, and at other times had lost their hooks and become calcified. Besides the heads, there were in the alveoli laminated calcareous corpuscles and red hæmatoidin crystals, and occasionally also accumulations of yellowish-brown bile-pigment. That the heads are contained in brood-capsules is asserted only by Morin.[1]

We have already mentioned that the bladders, both large and small, have but rarely a regular spherical shape. Not only does the wall of the latter often appear to be indented and folded, but one not unfrequently finds bladders which are more or less deeply constricted in the middle, while others have lateral protrusions of varying number and size, which occasionally project outwards almost like a berry (Fig. 334).

As Kuhn has already stated, similar racemose forms are found in the common *Echinococcus* of cattle,[2] except that in this case the protrusions are larger, and attain an average size of 1 cm. I have inserted a drawing of this racemose *Echinococcus*, but unfortunately I am unable to state its origin. The protrusions together enclosed a single undivided hollow space, although the communication was in many cases effected only by means of a narrow canal. I am not certain, indeed, whether there were not also some isolated bladders in the neighbourhood of the worm.

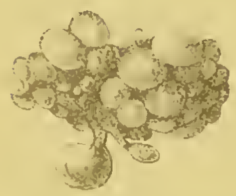


FIG. 334. — *Echinococcus racemosus* (nat. size).

If we think of this *Echinococcus racemosus* as enclosed in a common thick stroma, in which the individual protrusions have each their own alveolus, it is seen that the only difference between it and *E. multilocularis* is in regard to the size of the separate parts.

I think this resemblance justifies us in concluding that the *Echinococcus multilocularis*, like *Cysticercus racemosus* (p. 554), originates from primarily simple bladder-worms, and not, as was sometimes supposed, from a large number of isolated *Echinococci*.

It is still, however, a moot-point whether the individual bladders of *Echinococcus multilocularis* are always and exclusively formed by inflated protrusions of the wall. As Virchow had before observed, I have often seen upon the surface of the bladders tuft-like and club-

[1] He says that only some of the heads were found in the brood-capsules, the majority being situated directly on the parenchyma layer (*loc. cit.*, p. 31).

[2] See, for example, the case of Mégnin above mentioned (p. 614). Krabbe also asserts that in the liver of the sheep he has often found the *Echinococcus*-bladder "often somewhat branched"—*Archiv f. Naturgesch.*, Jahrg. xxxiv., Bd. i., p. 120, 1865.

shaped appendages, sometimes of microscopic size, which enclosed a cord-like continuation of the parenchyma, and in their thickened end not unfrequently exhibited an independent concentric lamination. Sometimes the granular cord in the interior was interrupted, so that the club-like end then enclosed a small cavity, with a granular mass in the interior.

I think I am not wrong in interpreting these appendages as stolons or sprouts—that is to say, as structures which are equivalent to the previously described buds, although they differ from them in so far as they are continuations not only of the parenchyma, but also of the cuticular wall of the mother-bladder. The ultimate fate is the same in both cases, for the terminal portion of the sprout gradually becomes a daughter-bladder, which not unfrequently even becomes constricted off, and is then associated with the others as an independent structure. Klebs, indeed, is of the opinion that the separate bladders of *Echinococcus multilocularis* are still connected with each other, but I have repeatedly convinced myself of the opposite, although there is no doubt that in many of the bladders, and perhaps even in the great majority, there is a continuous connection (at least of the cuticle).

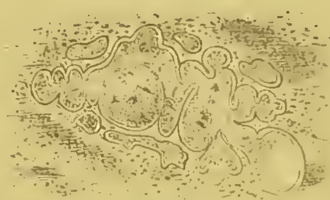


FIG. 335.—*Echinococcus multilocularis.* ($\times$ 30.)

According to all appearance, the bladders of the multilocular *Echinococcus* originate from smaller or larger sacculated masses of parenchyma, which are formed in the manner already described from a folding of the cuticular wall and subsequent marginal growth. I have even occasionally observed in my preparations what looked like interlamellar buds.[1] To this category, perhaps, we ought also to refer small sacs surrounded with a special cuticular layer, which Virchow found in the wall of the larger bladders, and which he regarded as originating in the interior of the above-mentioned stellate network. In general, the multilocular *Echinococcus* does not exhibit, in regard to its proliferation, any important differences from the other forms. Yet both Virchow and Schiess assert that in some bladders they have observed several generations encapsuled one within the other.

The new bladders formed on the external surface remain, however, but rarely within the alveolar space occupied by the mother-bladder. Usually, they very soon press into the adjacent and comparatively less compact stroma, forming a small special cavity, which always closes after the separation of the buds, and then appears as

[1] Morin also describes these interlamellar buds, and, as we have already mentioned, sometimes even finds heads in them.

though the inhabitants had originated within it. The resemblance of this to the primary *Echinococcus* cavity is all the more striking, since the inner surface of the alveolus is covered with the same irregularly formed granular cells which we have already described. Between these one finds numerous fatty granules, hæmatoidin crystals, and clot-like structures, which become more abundant the nearer one approaches the ulcerated parts. Nor is there any lack of bile-pigment and salts of lime. The latter sometimes impregnate the wall of the cavity so abundantly (as is occasionally observed in other bladder-worms), that they may be extracted from the alveolus in the form of a more or less continuous shell. The intervening connective tissue also often becomes the seat of a calcareous deposit, in which localities the structure of the connective tissue is gradually destroyed. The fibrils disappear, the fundamental substance becomes turbid and granular, until the alveolar wall is ultimately changed into a caseous mass, the destruction of which is followed by ulceration and formation of lacunæ.

If it were necessary to corroborate the parasitic nature of the so-called "alveolar colloids" by further facts, we might refer to the chemical character of the bladder-walls, which exactly correspond to the cuticular membranes of the usual *Echinococcus*-bladders, of which they are also the histological equivalents. We have already learned from Frerichs the essential chemical properties of this substance, and have seen that it belongs neither to the proteids nor to the gelatinous tissues. The recent and minute investigations of Lücke[1] have confirmed these statements, and have proved that the cuticle of the *Echinococcus* is chitinous, although it differs from the usual Arthropod chitin in possessing less power of resistance against caustic alkalies and boiling water. There are, however, many differences between the older and younger *Echinococcus*-bladders, not only in their behaviour towards reagents, but also in their elementary composition,[2] and in the analysis of their ash.[3] By the proper application of sulphuric acid and hot water, the cuticle of the *Echinococcus*, like ordinary chitin, may be partly changed into grape-sugar, although the amount

[1] *Archiv f. pathol. Anat.*, Bd. xix., p. 189, 1860.

[2] The results of Lücke's analyses are :—

		Old Bladders.	Young Bladders.
Carbon	=	45·342	44·068
Hydrogen	=	6·544	6·707
Nitrogen	=	5·1493	4·478
Oxygen	=	42·9547	44·747

[3] This difference in the ash (young bladders = 15·79 per cent., old bladders only = 0·28), which consists principally of salts of lime, is so striking, that we feel inclined to ask whether the membranes were in both cases equally freed from the inner parenchyma and from the calcareous corpuscles ; but of this Lücke does not inform us.

of sugar formed (50 per cent.) shows that they still contain a small quantity of nitrogenous substance ("hyalin," Hoppe-Seyler).

From Lücke's investigations, it appears that grape-sugar is also a somewhat common constituent of the fluid contained in the *Echinococcus*-bladder, and that it occurs constantly in those cases in which the parasite lives in or near the liver. It is, however, highly improbable that this sugar is a product of the chemical metamorphosis of the *Echinococcus*-cuticle. It is much more probable that it originates in the liver and its veins, especially as the absorptive capacity of the *Echinococcus*-bladder is very great, and as the investigations of Barker and Queckett in a case of *Echinococcus* in the kidney have proved the presence in the interior of the bladder of crystals also of uric acid, oxalic acid, calcium triple phosphates, and other earthy constituents of the urine.[1] In this way may be explained the presence of cholesterin crystals, which are often found in enormous numbers in the fluid of *Echinococci* from the liver, as also the occurrence of hæmatoidin crystals, which have frequently been observed in the latter, and are always to be found in the multilocular *Echinococci*. A case investigated by Davaine contained hydatids, only some of which contained these crystals, but all of which were furnished with calcareous corpuscles of exactly the same deep red colour.[2] The presence of these blood constituents indicated an ecchymosis, which had taken place some time previously, by a rupture of the vessels passing through the wall of the cyst.[3] In *Cysticercus pisiformis* and *C. tenuicollis* I have under the same circumstances occasionally seen the whole fluid of the bladder of a blood-red colour, and so may it have been in these *Echinococci* before the hæmatoidin crystallised out.[4]

It has long been known that in its normal condition the fluid within the *Echinococcus* is almost entirely devoid of albumen, and therefore does not coagulate on boiling. This also corresponds with its low specific gravity (1009 to 1015). But instead of albumen it has abundance of leucin and tyrosin. Heintz has also proved that it contains succinic acid, which is found in hardly any other living organism. Lücke is indeed of opinion that the body in question does not quite correspond to succinic acid; but Naunyn has in the meantime confirmed Heintz's discovery, and has also found inosite in the fluid.[5] Half of the 1·5 per cent. of inorganic substance consists of common salt.

[1] Barker, "On Cystic Entozoa in the Human Kidney," p. 9, London, 1856 (quoted by Davaine).

[2] *Mém. soc. biol.*, p. 107, 1855.

[3] In this way is also explained the constant occurrence already mentioned of hæmatoidin crystals in the ulcerating multilocular *Echinococcus*.

[4] Davaine indeed reports a case in which *Echinococci* of a red colour were expectorated.

[5] *Müller's Archiv f. Anat. u. Physiol.*, p. 921, 1863.

Occurrence and Medical Importance.

Davaine, "Traité des Entozoaires," pp. 359-620, pp. 644-656.
Neisser, "Die Echinococconkrankheit:" Berlin, 1877.
Marie Prougeansky, "Ueber die multiloculäre ulcerirende Echinococcusgeschwulst in der Leber," Inaug.-Dissert., Zurich, 1873.
Boecker, "Zur Statistik der Echinococcen," Inaug.-Dissert., Berlin, 1868.

Among human parasites none can compare with the *Echinococcus* in the variety of its occurrence. Even the *Cysticercus cellulosæ*, which, on account of its residence in such different organs, has been rightly described as one of the most widely distributed helminths, is in this respect far behind the *Echinococcus.* There is hardly an organ of the human body in which it does not occasionally dwell—even the bones being occasionally infested by it.

All these organs, however, do not contain the worm with equal frequency. Like *Cysticercus cellulosæ*, the *Echinococcus* has favourite situations, and others which it visits less frequently, or perhaps only rarely. The favourite seats of the two parasites are, however, very different. The intermuscular connective tissue, for which the *Cysticercus* has a special preference, is but rarely the seat of the *Echinococcus.* In the brain, and especially in the eye, the *Cysticercus* is found far more frequently than the *Echinococcus;* this in its turn has a special preference for the viscera, which are avoided by the other, and above all, for the liver. Neisser, who has given a very accurate and almost complete account of the cases of *Echinococcus* hitherto observed in man, and who has increased the 367 observations[1] of Davaine (in 1860) to the large number of 986, mentions in his table no fewer than 451 *Echinococci* in the liver, so that these almost amount to half of all the cases recorded. After the liver in the scale of frequency, we find the lungs and pleura with eighty-four distinct cases, the kidney with eighty, the muscles and dermis (including the orbit) with seventy-two, the brain with sixty-eight (spinal cord with only thirteen), the female genitalia (including the mammæ) with forty-four (the male with only six), the true pelvis with thirty-six, the circulatory apparatus with twenty-nine, the spleen and bones with twenty-eight, the eye with three, and so on. Finsen, whose observations only extend over 255 patients, all of them Icelanders,[2]

[1] Boecker, who only makes use of materials from the Berlin Hospital, reckons altogether thirty-three cases. Of the earlier accounts, I mention particularly von Lüdersen, "Dissert. de hydatibus," Göttingen, 1808, and von Rendtorff, "De hydatidibus in corpore humano repertis," Berolinæ, 1822.

[2] "Bidrag til Kundskab om de i Island endemiske Echinococcer," *Ugeskr. for Læger*, Bd. iii., p. 71, 1867.

estimates the number of *Echinococci* in the liver at 69 per cent., and those of the abdominal thoracic viscera (lungs only 3 per cent.) altogether at 95 per cent., so that the extravisceral occurrence appears to be rather the exception.

As a rule, the number of *Echinococci* which attain development in man is limited to one or to very few, which are then found either in neighbouring organs, or more commonly in the same. Where only one organ suffers, it is almost always the liver. But curiously enough in man this organ is but rarely tenanted by a large number of *Echinococci*, such as one sometimes finds in the animals used for food, and especially in swine, whose liver is sometimes penetrated by hundreds of distinct *Echinococcus*-bladders.[1] There are, indeed, instances in man where the number of *Echinococci* considerably increases and the sphere of distribution becomes more extensive. In all cases of multiple *Echinococci* the liver is probably one of the affected organs, but the majority of the parasites are nevertheless usually found in other parts, especially in the omentum and peritoneum, but also in the lungs, spleen, and kidneys. Thus Wunderlich[2] describes a case in which, besides a hydatid *Echinococcus* in the liver as large as a child's head, there were in the spleen, in the retro-peritoneal space, in the omentum, behind the cæcum, in Douglas' pouch, twelve other bladders, varying from the size of an apple to that of a fist, while under the mesenteric coating of the small intestine there were about half a hundred "dried" *Echinococci*, whose size varied from that of a poppy-seed up to that of a bean.

In another case reported by Davaine,[3] the liver contained a large number of small *Echinococci*, which projected only slightly from the surface, but beside these were two larger sacs, of which one contained at least three pounds of fluid, with many daughter-bladders, some of them of the size of an egg. There were also numerous larger *Echinococcus*-bladders in the true pelvis, between the bladder and the rectum, in the gastro-hepatic and gastro-splenic ligaments, in the wall of the transverse colon, and in the neighbourhood of the cæcum, besides numerous small bladders, some only the size of peas, under the peritoneal coating of the intestine.

In the absence of exact reports it is difficult to determine with certainty the number of the bladders in such cases. Wunderlich

[1] Through the kindness of Professor Nitsche in Tharand, I lately received half of a pig's liver, which was penetrated by hundreds of (sterile) *Echinococci*, about the size of nuts, whose cysts lay so close to each other that the liver substance was largely compressed, and in spite of its weight of thirty-six pounds, was really little more than a trabecular structure of connective tissue, in which the bladder-worms were embedded.

[2] *Archiv f. physiol. Heilk.*, p. 283, 1858.

[3] *Mém. soc. biol.*, p. 106, 1857.

designated the above-cited case as exhibiting "countless *Echinococci*," but in point of fact they are reduced—apart from the secondary hydatids of course—to less than a hundred. It seems to me also that the "thousands" spoken of by Küchenmeister in the last edition of his work on parasites are the result of a similar excessive estimate.[1]

But even if the number should not be much over a hundred, it is large enough to suggest the question whether we have here the result of a single infection.

When we consider that the multiple *Echinococci* exhibit usually very considerable variations in the size and development of the bladders, we are inclined at first to suppose that a repeated importation of the *Echinococcus*-brood has occurred. The above-mentioned disparities would then be readily explained by a supposition not in itself improbable. Nevertheless I believe that a repeated infection with the *Echinococcus*-brood must be very rare, for even a single infection demands the co-operation of manifold factors. In certain cases of *Cysticercus cellulosæ* we might admit the supposition without difficulty, but here the conditions are essentially different, since the *Tænia solium,* which furnishes the material for infection, is much nearer to man than the *T. echinococcus,* whose eggs only reach us from the dog.[2]

If, then, the multiple *Echinococci* are to be referred to a single infection, it does not follow with absolute certainty that they are all of the same age. The *Echinococcus*-bladders have, as we know, the power of proliferation, and even of manifold proliferation; it is therefore possible than in the multiple *Echinococci,* in addition to the first immigrants, we have their descendants.

We think first of the possibility of an exogenous proliferation—a process which does indeed come into consideration in explaining the multiple *Echinococci.* But this supposition is only admissible when the bladders, large and small, lie close beside one another, or at short intervals. But, as a rule, the multiple *Echinococci* are scattered over different, often widely separated organs, so that this explanation is insufficient. For such cases one must refer to the observations of Naunyn and Rasmussen, who have shown that heads and brood-

[1] In the description of one of the two cases observed by Küchenmeister we read as follows (*loc. cit.*, p. 214) :—"All the organs of the pelvic cavity were filled with *Echinococcus*-bladders from the size of a hazel nut or walnut to that of an apple or a fist. There must have been towards a thousand." No enumeration, however, is made, and the approximate estimate cannot be right, since 1000 bladders, even of the size of a walnut, would fill about a cubic foot, more than the whole contents of the pelvic cavity. Even the "many hundreds," to which Küchenmeister has now reduced them, must surely be still too high an estimate.

[2] I repeat that Küchenmeister's supposition of the occurrence of *Tænia echinococcus* in man (and also in the pig, the ox, the sheep) is quite baseless.

capsules do sometimes change into hydatids. Of course there is the further difficulty that one must suppose that the primary *Echinococcus* has first opened into a vessel, and liberated its brood-capsules or its heads into the blood, which then transports them hither and thither. The possibility of this would admit of experimental verification. I regret that I have found no opportunity for so doing, and that the more since I do not share Neisser's *à priori* objections to this mode of explanation, although I am but little inclined to lay much stress on it.[1]

It seems to me most probable that the multiple *Echinococci*, or at least the great majority of them, are the result of a single infection, but of one which furnished not one but many embryos. The above-mentioned differences in size and development are easily explained by remembering that the embryos are exposed to diverse external conditions, so that some grow more quickly, and to a larger size than others. This idea is confirmed by experience. In examining the animals upon which I had experimented, I have often found considerable differences in the size and development of bladders, which originated from the same feeding. If such differences be noticeable in worms only a few weeks old, how much greater must they be in the course of a life of years or perhaps decades.

Probably it is not only multiple *Echinococci* which owe their origin to an invasion of numerous embryos. Among the cases of solitary *Echinococci* it may be that many originated from a more or less abundant infection. We know, too, that it is not exclusively the number of imported germs which determines the issue of a helminthological experiment, but also the sum total of the circumstances under which the introduction and development of the young brood occurs. Most emphatic, perhaps, is the fact that the *Cœnurus*, which is generally found solitary, is not always so from the first. We may therefore with some probability suppose that the solitary *Echinococcus* often acquires that characteristic by a sort of selection. There are at first, perhaps, a large number of young *Echinococci*, of which one (or a few) gradually predominates over, and finally suppresses, the others. When we consider that the disease usually calls for attention only after persisting many years, we can understand why but few of these degenerated *Echinococci* have been found. I may take this opportunity of recalling the fact that in certain organs the *Echinococci* are found associated in large numbers much more frequently than in others.

[1] I must leave it undecided whether Morin (*loc. cit.*, p. 34) is right in claiming an embolic origin for the small *Echinococci* found by him in the lung of a patient infested with a multilocular *Echinococcus*. He leaves the nature of the embolism undiscussed, but it appears as though he were thinking more of daughter-bladders than of heads or brood-capsules.

While it is extremely rare that more than five or six *Echinococci* develop in the liver or lungs of man—(there are a few cases where the liver contained twenty)—one finds in the peritoneal coat of the abdomen or in the omentum hardly a single example of a solitary *Echinococcus*.

After what has been proved in regard to the natural history of *Tænia echinococcus*, there can be no doubt as to the origin of the *Echinococci*. The *Echinococcus*-bladders are descended from the tape-worm, and where they occur an importation of the tape-worm brood must have preceded, *all creatures suffering from Echinococcus, whether man or beast, must in some way or other have become infected with the eggs or proglottides of the Tænia*, and have had the enclosed embryos liberated by the action of the digestive juices. After their liberation these embryos must have bored through the intestinal walls,[1] and have more or less directly reached their subsequent position. This internal wandering may be effected through the blood-vessels or lymphatics, and this view is supported by the preference of the worms for the liver, which is rendered easily accessible by virtue of the portal circulation. That all the *Echinococci* are not found in the liver is no contradiction, because the embryos may readily pass by the lymphatics into the venous system.

Since the *Tænia echinococcus* inhabits especially the intestine of the dog, and since the dog is the only host known to us which comes into close association with man and domestic animals, *we can hardly be in error if we regard it as the only source of the Echinococcus disease.*

We need hardly show how cattle, &c. may infect themselves with the eggs or proglottides of *T. echinococcus.* The proglottides voided by the dog so constantly and in such numbers—for the tape-worm, as we know, lives socially, and often occurs in thousands—are either eaten with the dung, as by swine, or are carried by their own and by external movements on to substances which serve as food, and thence into the intestine of cattle and other herbivorous animals. Sometimes only the eggs and not the proglottides are thus transported, but the result is the same, provided the eggs have not in the meantime lost their power of development, or fallen into an unfavourable environment.

But how are they introduced into man. Primarily, of course, and most frequently, in consequence of accidental contact, as we explained, in connection with *Cysticercus cellulosæ.* In the latter case the infecting material has its origin in man himself, in the present case in an animal which lives near man, sharing lodging, food, and sometimes even bed

[1] I cannot support Neisser's idea that the six-hooked embryos are quite passive in their transmission through the tissue, like silver grains in Argyriasis, since they are by no means so motionless as Neisser seems to suppose. See p. 322.

with him; but this point of difference is of little consequence. In the latter case, as in the former, both proglottides and eggs may in many ways be carried in food or on the hands to the mouth, and thus reach the intestine; and that the more readily, since dogs are fond of licking the hands or faeces of their masters, and equally fond of snuffing at the anus or dung of other dogs. They may thus be in a sense intermediate hosts, and yet themselves remain free from the adult *Tænia.*

Too familiar association with dogs is, indeed, anything but safe, and that especially in places and under circumstances (such as sausage-manufactories and slaughter-houses) where the dogs can readily obtain portions of *Echinococcus*-bladders, and develop them into sexually mature tape-worms. We must prevent dogs from licking us, banish them from room and kitchen, keep them clean, and see that their excrement is as far as possible removed. Further suitable precautions should be taken to prevent an infection with embryos of *Echinococcus;* the dogs should be kept away from places where the bladders are thrown carelessly away, or even given to dogs as tit-bits. The careless disposal of these "water-bladders," and the unnecessarily large number of dogs, have most to do in perpetuating and propagating one of the most severe and dangerous forms of helminthiasis.

From the universal distribution of the dog, as well as of herbivorous domestic animals, that is to say, of those creatures which mainly facilitate and provide for the cyclic development of *Tænia echinococcus,* it is easy to suppose that the cystic worm is everywhere developed in man. Experience has completely established the accuracy of this conclusion, for we now know not only of cases of *Echinococcus* from all parts of the world, but are also acquainted with the fact that in some countries the disease is endemic, and endangers the health and life of the inhabitants more than any other illness.

Among these countries is Iceland, where the *Echinococcus* disease (the so-called "liver plague") is so frequent that the Danish government was compelled to send thither a special expert to investigate its causes, and check its further spread by suitable arrangements. Although indigenous there for centuries, the parasitic nature of the disease was only discovered about thirty years ago, indeed, by Schleisner,[1] who spent two years in the island for medical purposes. On the ground of his own investigations and of the testimonies of the local physicians, he estimated the number of patients suffering from hydatids at one-sixth to one-eighth of the whole population, that is to say, 10 to 15 per cent., or altogether about 10,000 persons. Although Thorstensen, who practised in Iceland for more than twenty years, also believes that

[1] "Island, undersögt fra et lægevidenskab. Synspunkt:" Kjöbenhavn, 1849.

every seventh individual suffers from this disease, it has gradually been established by means of more accurate statistics that these early statements were exaggerated.[1] According to the reports of the medical officer Finsen, who, in his district, which comprehended a seventh part of the whole island, had a yearly average of between 700 and 800 patients, there were among that number twenty-four persons infected with *Echinococcus*, and thus about 3 per cent. Among the 10,000 inhabitants of this district, he knew altogether 119 *Echinococcus* patients (about 1·2 per cent.), and this of course without taking into account those in whom the development of the parasite had not yet given rise to pathological disturbances; when we further consider that it is probable, especially in regard to the more remote parts of the district, that all the patients had not come to the knowledge of the physician, the number of the real *Echinococcus* patients in Finsen's district (in the north of Iceland) may be estimated at about 2 per cent. of the population. It certainly appears as though the *Echinococcus* were more frequent in some of the agricultural districts, and especially in the east of Iceland, but Krabbe has shown that this preponderance is almost compensated by the relative rarity of the parasite in those neighbourhoods where there is more fishery and trade, as in Reykjavik, so that the total number of the Icelandic patients can hardly be estimated at more than 1500 ($\frac{1}{46}$) of the population. Still that is a very large number, much larger at any rate than is found anywhere else.

In Iceland *Echinococcus*-bladders are much more frequent in oxen and sheep than in man;[2] but, although present in considerable numbers in these animals, they hardly ever attain the same size as in man, and as they frequently shrivel up and calcify, they do not cause such important disturbances of health.

As the inhabitants are chiefly engaged in the rearing of cattle, the number of these animals is so great that there are eleven for every man, as opposed to 1·8 in the kingdom of Denmark; and, as the flesh of the slaughtered animals is usually handled in a very careless, disorderly, and uncleanly manner, it is not difficult to believe that *Tænia echinococcus* is of most frequent occurrence among the dogs.

[1] On this subject see in *Ugeskrift for Läger* (1862-66), a paper on the Icelandic *Echinococci*, which is translated by Krabbe in *Archiv f. pathol. Anat.*, Bd. xxvii., p. 225, and one on the *Echinococci* of the Icelanders, *Archiv f. Naturgesch.*, Th. i., p. 110, 1865. [This subject has been recently treated by Fonassen ("Echinokokkensygdomen belyst ved Islandske Lægers Erfaring:" Kjöbenhavn, 1882), who estimates the number of patients on the average at 1·3 per cent. of the population.—R. L.]

[2] Hjaltalin, who, in 1870 (Dobell, "Report on Iceland," London, 1870) still maintained that one-sixth to one-seventh of the population suffered from *Echinococcus*, estimates the number of sheep infected with the parasite at one-fourth.

Krabbe found it to be forty-seven times more frequent in the dogs of Iceland than in those of Copenhagen, and discovered its presence in about a third of the animals which he investigated, or in 28 per cent., as against 0·6 per cent. in Copenhagen. Thus, when we consider, in conclusion, that in Iceland there is a dog for every eleven persons (in France for twenty-two, in Baden for forty-nine, in England for thirty-five, and in Scotland for seventy-four), and that all these dogs have intercourse with men and cattle, it is easy to see that millions of eggs must be daily distributed by these animals, and that although the majority of them may be destroyed, the remainder, which reach their destination, are quite sufficient to give rise to the disease to the above-described extent. The transmission of the embryo must be facilitated by the want of cleanliness, which is especially prevalent among the country people, and which is increased by the conditions of their life, and particularly by the long duration of the winter, which is spent by some in the same rooms with the dogs. The carelessness with which the Icelanders carry on their intercourse with these animals must also frequently lead to infection, for they even go so far as to allow their wooden dishes to be licked clean by the latter, instead of washing them. Another fact to be taken into consideration is, that the cool and damp climate preserves the vitality of the dispersed germs much more effectually, and for a much longer time, than would be the case under other circumstances.

Wherever similar circumstances occur, the *Echinococcus* disease attains a similar distribution. According to Richardson,[1] it is so in Australia, among the inhabitants of the district of Victoria, and especially among the shepherds, also among the Burätis, whom we have already had occasion to mention as the hosts of *Tænia saginata*. At all events, Kaschin states that in nearly all the *post mortem* examinations which he made, he found "hydatids" in the liver and heart which could hardly have been anything else than *Echinococci*.[2] The accounts which are given of the mode of life and customs of this nomadic people support this conjecture. We learn, for example, that in unfavourable weather, and particularly in winter, the Burätis live in the same tents (*jurten*) as the cattle and dogs, and in the most loathsome state of filth and uncleanliness, since they wash neither their dishes nor their own bodies, and wear their clothing until it falls to pieces.

[1] *Edinb. Med. Journ.*, p. 525, 1867. The eating of raw flesh, which is, according to Richardson, the means by which the shepherds are infected with *Echinococcus*, cannot, of course, be so unless the dogs have by chance deposited on the flesh the proglottides and eggs of their *Tæniæ*. [See also Thomas, "Hydatid Disease, with special reference to its Prevalence in Australia," Adelaide, 1884: in Victoria *Echinococcus* occurs once in 18,800; in South Australia once in 23,000 inhabitants.—R. L.]

[2] *Petersburg Medical Journal* (Russian), vol. i., p. 366, 1861.

In Algiers the *Echinococcus* seems somewhat widely distributed both among the aborgines and Europeans. It is also frequent in Egypt, but in America, so far as we know, it is rare. In Europe we know of the occurrence of the *Echinococcus* in almost every country. It is found, for example, in Italy, France, England, and especially in Germany, from which the accounts are so numerous, and so numerically exact, that they alone furnish us with tolerably satisfactory statistics. In the literature of other countries we search almost in vain for any numerical statements. We can indeed hardly learn anything more than that, in 200 *post mortem* examinations made by Leudet in 1855 in the hospitals of Rouen, he found *Echinococcus* six times. I do not know what foundation there is for the statement of Cobbold, that in England there are every year about 400 *Echinococcus* patients.[1]

In his reports on the clinical institutes and hospitals of Germany, Neisser[2] gives the number of cases as 153, and as this number was found in about 500,000 persons who had been examined, the percentage may be estimated at 0·03. If we only take into account the results of the *post mortem* examinations (ninety-five cases out of 13,882), we shall of course obtain a much larger proportion (nearly 0·7 per cent.), and if we add to this the 1812 autopsies, with two cases of *Echinococcus*, not mentioned by Neisser, in the Erlangen Clinical Hospital, and also the 2002, with seven cases, in Dresden,[3] the number is raised to nearly 0·6 per cent. Obviously it is principally the reports coming from the north and middle of Germany (Rostock, Berlin, Göttingen, Dresden, Breslau) that affect the result, with their ninety-four cases of *Echinococcus* in 12,800 autopsies, while observations made in Prague, Vienna, and Zurich (six cases in 2916 examinations,—thus about 0·02 per cent.) make hardly any difference.

The *Echinococci* are thus considerably more frequent in the middle and north of Germany than in the south, and the number of patients even appears to increase as we go northwards. Yet we find from the foregoing reports that among 261 *post mortem* examinations made in Rostock[4] there were no fewer than twelve cases of *Echinococcus*, thus giving a per-centage of 4·59, which is larger than in Iceland. On

[1] *Journ. Linn. Soc. Lond.*, vol. ix., p. 292, 1867.

[2] *Loc. cit.*, p. 36.

[3] Müller, "Statistik, &c.," p. 14.

[4] [It has recently been most unexpectedly shown that the *Echinococcus* is truly endemic in Mecklenburg, especially its northern and eastern districts, as also in the neighbouring districts of Pommerania. The disease seems to be most widely distributed in Rostock, where there is one patient in every 1414 inhabitants: the whole country shows one patient in every 18,800 inhabitants. See "Beiträge Mecklenburger Aerzte zur Lehre von der Echinococcuskrankheit" herausgegeben von Madelung: Stuttgart, 1885.—R. L.]

the other hand, the number of observations is so small, that it is quite possible there has been some error.

It is almost unnecessary to say that the data which we have obtained by clinical observations must not be held as directly applicable to the general population. The proportion in which the *Echinococcus* occurs in the latter cannot at present be even approximately estimated; but at any rate it is much less frequent than *Cysticercus cellulosæ*,—probably even in those districts of Germany in which it is relatively most abundant.

The explanation of the variable frequency of the *Echinococcus* is always to be found in the different occupations and modes of life of the inhabitants. The extent to which cattle and sheep are reared, the number and treatment of the dogs, and the varying degree of cleanliness, are the principal factors by which it is determined; and this is true not only of the different countries which are geographically and climatically distinct, but also of much more restricted limits. This explains why the *Echinococcus* occurs more rarely in towns, and especially in large towns, than in the country, where the slaughtered meat is less strictly inspected, and the dog not only has more frequent opportunities of becoming infected with *Echinococcus*-heads,[1] but is allowed more unrestricted intercourse with man. Similarly, it appears that herdsmen and shepherds, with the members of their family, furnish an unusually large contingent to the number of *Echinococcus* patients, and at any rate a much larger one than seamen, among whom, as has already (1846) been shown by Budd, this bladder-worm is extremely rare. The fact mentioned by Busk, that the lower classes are more frequently subject to infection than the higher, must be ascribed essentially to the want of order and cleanliness among the former, and thus to circumstances which also affect the frequency of *Cysticercus cellulosæ*. On the other hand, we know of persons of a higher rank who have been infected with *Echinococcus*, usually, indeed, in consequence of two close intercourse with pet dogs. To the same circumstance is perhaps to be referred the somewhat mysterious preponderance of female patients, which, according to the statistics of Neisser, amounts to nearly a third (210 : 148), and is all the more striking, since it will be remembered that in *Cysticercus cellulosæ* we had to note exactly the opposite proportions. It is, however, true according to Finsen that this preponderance of the female *Echinococcus* patients is also found in Iceland (255 : 181), where no pet dogs are kept.[2]

[1] With this agrees the statement of Krabbe, that the dogs in which he found *Tænia echinococcus* came principally from the suburbs of Copenhagen, *Archiv f. Naturgesch.*, *loc. cit.*, p. 120.

[2] We may take this opportunity of remarking that the cases hitherto observed of

A fact that is still more remarkable than this preponderance of the female *Echinococcus*-hosts, is that more than half of the cases of *Echinococcus multilocularis* which have hitherto been observed in man (nineteen cases among thirty-five, according to Niesser) belong to Switzerland; and in Germany this form has been found almost exclusively in the south, so that a case observed in Dorpat is quite an exception. Yet these countries are precisely the ones in which *Echinococcus* is otherwise rare. We can hardly agree with Klebs in supposing that the reason of this peculiar phenomenon is to be found in the prevalence of cattle-breeding, since the most that could be inferred from this would be a frequent occurrence of the *Echinococcus*. Perhaps, after we have learned the causes that give the *Echinococcus multilocularis* its peculiar form,[1] we shall find a better explanation. In the meantime we have so little light on the subject that we do not even know whether the determinant factors are to be found in the worm itself, or, as is certainly more probable, in the condition of the environment (abode, nature of the enveloping cyst, &c.).

In regard to the age of patients suffering from *Echinococcus*, it is quite certain from the reports of Neisser that, like *Cysticercus cellulosæ*, the parasite occurs most frequently in persons between twenty and thirty. No fewer than 55 per cent. are found within this period, while the rest are distributed over various other ages, up to fifty and sixty, but always occur in greatest numbers near the former age. It is doubtful whether the infection also takes place within this time, especially as we know that the *Echinococcus* grows but slowly, and usually only causes great disturbances of health after an existence of some years. For the same reason it is extremely rare for it to occur in early childhood. Finsen operated on a boy of six, who had harboured the *Echinococcus* since his first year; and Thorstensen reports the case of a child of four, in whom the extirpated bladder-worm (*E. hydatidosus*) had already attained the size of a child's head.[2]

So far as I know, these are the youngest, reliable cases of *Echinococcus* patients. It is, indeed, stated by Hammer that, in the case of a newly born child, whose much distended abdomen proved a

multiple *Echinococci* have occurred almost exclusively in the female sex. Küchenmeister connects this fact with the looseness of the peritoneal covering of the female sexual organs, which he thinks possibly favours the development of the parasite.

[1] Morin finds the explanation of this phenomenon in the specific nature of the *Tænia* belonging to the *Echinococcus multilocularis*, but, except the peculiar geographical distribution, he can urge nothing in support of this view beyond the fact that the feeding experiments which he made with the multilocular *Echinococcus* yielded no positive results (*loc. cit.*, p. 37).

[2] Krabbe, *Archiv f. pathol. Anat.*, *loc. cit.*, p. 232.

hindrance to birth, and had to be opened, he found hydatids to be the cause of the swelling,[1] but this has probably nothing to do with the *Echinococcus*. The same may be said of Cruveilhier's case of a child twelve days old, in whose liver there are said to have been some calcified hydatid cysts.[2] The bladders found by Heyfelder[3] in the placenta and umbilical cord of a fœtus of seven months, are to be referred to a so-called "hydatid mole," which, as is well known, has nothing in common with the *Echinococcus*.

The slow growth is quite sufficiently shown by my reports of the dissections of animals which had been used for rearing the *Echinococcus*. But under some circumstances this growth can be directly observed in man. Velpeau, for example, reports a case of *Echinococcus* in the neighbourhood of the shoulders, which in six months grew to the size of a small walnut. In another case an *Echinococcus* similarly situated grew within a year to the size of a fist.

The growth of the *Echinococcus* is, however, by no means the same in all cases. It is affected by the position and character of the attacked organ, by the form of the worm, and by individual circumstances of the most manifold nature. The hydatid *Echinococcus* seems to have the longest and most continuous growth, and in time often attains quite an enormous size. It is true that this requires years, and even decades. We have already mentioned such a case, and several similar ones are recorded in literature.[4]

Thompson treated an *Echinococcus* of very large size, the first traces of which had been observed thirty years before; and Raynal operated on a woman, in whom the swelling had gradually spread during forty-three years over a considerable portion of the face, and attained the size of a child's head. On incision numerous daughter-bladders shot forth, which had a perfectly healthy appearance, and some of which were only the size of peas.

As a rule, however, the *Echinococcus* comes sooner to an end, and usually by causing the death of its host. Perhaps the great danger of the *Echinococcus* is best shown by a paper of Barrier's,[5] in which he mentions that of twenty-four cases with which he was somewhat exactly acquainted, more than half terminated fatally during the course of the first five years. Three *Echinococci* had an existence of less than two years, eight of two to four, and four of four to six. Of the rest, three caused death after six to eight years, two after eight years, and four after fifteen, eighteen more than twenty and more

[1] *Neue Zeitschrift f. Geburtskunde*, Bd. iv.
[2] "Traité d'anat. pathol.," xxxvii., p. 6.
[3] *Schmidt's Jahrb.*, p. 324, 1834.
[4] See Davaine, *loc. cit.*, p. 384.
[5] "De la tumeur hydatique du foie," p. 36, Thèse Paris, 1840 (quoted by Davaine).

than thirty years respectively. The reports of Neisser, based upon fifty-four cases, only differ in that comparatively the greatest number of fatal cases occurred within the first two years (that is to say, from the discovery of the parasite, and without taking into account the time during which it had escaped observation).

The time which the *Echinococcus* disease takes to reach its termination depends upon various circumstances. Besides the greater or less rapidity with which the parasite grows, it is mainly determined by the physiological nature of the infected structure. But even in the samê organ the *Echinococcus* gives rise to a different prognosis according to its situation; thus, for example, it is by no means indifferent to the host whether a bladder-worm in the liver has developed in the neighbourhood of the great vessels, or among the yielding ventral coverings. Nor is the form of the parasite of little moment in this connection, as is evident from the constancy with which the multilocular *Echinococcus* leads to the death of the patient through the ulceration of the intermediate tissue.

So long as the *Echinococcus* is but of small size, the disturbances which it causes are trifling, unless it occur in a nerve centre, or, as is very rarely the case, in the eye. But as the parasite increases in volume, the seriousness of the disturbance increases. In itself painless, it gradually produces a feeling of pressure and heaviness, which continually augments. The affected organ becomes enlarged, and loses its previous form and character. The surrounding body wall is raised up, if it can yield to pressure, and the adjacent organs are displaced. At the same time there sets in a series of functional disturbances, which become more and more aggravated, and which, at first associated with the increasing intruder, not unfrequently spread to adjacent parts. The health of the victim becomes more and more completely undermined; nutrition suffers, circulation is disturbed, a condition of marasmus results, and finally death supervenes with symptoms of exhaustion, unless a previous dropsical or inflammatory attack bring it about sooner.

The special symptoms of the *Echinococcus* disease vary, of course, greatly according to the situation and size of the parasite. A parasite occurring in the liver produces different pathological results from those caused by one occurring in the kidneys or lungs. Even in the same organ the results are very various. The different modifications, as detailed by Davaine and Neisser, and discussed by Küchenmeister, cannot here be entered into fully; we must restrict ourselves to a few observations of more general interest.

In the first place it may be mentioned that the life-history of *Echinococcus* exhibits hardly any factors fitted to produce a direct and

specific influence on the organism which shelters it. It might certainly be supposed that the process of immigration would cause disturbances of this kind (and indeed Küchenmeister has lately expressed himself of this opinion), but these could only result from an unusually abundant infection, and this is almost excluded by the nature of the adult *Tænia*. In the next place, the irritation which the developing parasite produces in its surroundings, has as a rule no further consequences than the formation and thickening of the wall of the cyst[1] and the displacement of the surrounding tissue.

The danger of the *Echinococcus* disease, however, arises from the effects of the pressure of the growing parasite, and this pressure is moreover always increasing, since the growth of these worms, and particularly of the hydatid form, which is by far the most frequent in man, is almost unlimited. In this respect the *Echinococcus* is exactly like certain tumours, with which it was classed until the end of the last century, and for which (at least during life) it may be still easily mistaken.[2]

This also explains how it is that, when the *Echinococcus* remains small or dies early, it usually causes so little annoyance that its presence is perhaps only discovered upon *post mortem* examination. The frequency of these latent *Echinococci* may be seen from the fact that of twenty-two cases which Böcker collected from the results of the Berlin Charité Hospital, only nine had been diagnosed during life. Among twenty-three cases of *Echinococcus*, Frerichs found eleven latent, and Neisser found as many as thirty-one among forty-seven.

The first and chief consequences of the pressure are that the adjoining vessels and glandular passages are compressed and rendered impassable to a varying extent. Œdema, varicose veins, and congestions of various kinds, are thus very frequent accompaniments of *Echinococcus*.

This pressure is most constantly manifested when the parasite is developed in cavities with more or less firm limits, as, *e.g.*, in the thorax, where it occasions the most serious dyspnœa, or in the pelvic cavity, and especially in Douglas' pouch, where its pressure both anteriorly and posteriorly considerably impedes the passage of the urine and the expulsion of the fæces. In women *Echinococci* thus situated sometimes act as such hindrances to delivery that it can only be accomplished after the puncture of the bladder.

[1] We know cases in which this cyst wall (only in consequence of repeated inflammatory processes) had attained a thickness of several centimetres.

[2] Even distinguished authorities upon abdominal tumours, such as Spiegelberg, Dumreicher, Baum, and Esmarch, have made mistakes of this kind, and while endeavouring to perform ovariotomies, have found to their astonishment, instead of the degenerated ovary, an *Echinococcus*. As a rule a simple puncture will be sufficient to avoid such an erroneous diagnosis.

When the *Echinococci* develop within the bones, the latter are at first eroded in proportion to the growth of the parasite. Afterwards the walls become thin, and often to such a degree that a moderate blow is enough to cause a fracture. Thus Dupuytren mentions that in the case of a man who had a hydatid *Echinococcus* in the much enlarged medullary cavity of his humerus, the latter broke when he tried to throw. Sometimes the *Echinococcus* breaks through the hard coating at some point, and then expands among the surrounding soft tissues. This happens not only when the parasite is developed in the cancellous tissue of the bone, but also when contained within the enclosed cavities, if it be but near the boundary. The cases are by no means rare in which the *Echinococcus* of the thorax breaks through the ribs and expands between the muscles, or where that found in the cranial cavity breaks through the bones of the skull and expands in the antrum of Highmore or nasal cavity. Sometimes, instead of seeking an independent path, the clefts and foramina already present are utilised. Those especially are traversed which lead into the orbits, so that in consequence of the intrusion eyesight is often lost, exophthalmus ensues, or the eyeball is wholly destroyed.

In considering these phenomena, we must not forget that the *Echinococcus* in such cases is destitute of the firm connective-tissue cyst, which otherwise surrounds it, and prevents it from exercising a direct influence on the adjacent tissues. In this respect *Echinococcus* closely resembles the bladder-worms which also occur without a capsule in the serous cavities. Besides, we must remember that such a worm has, to an unusual degree, the power of adapting its growth to its external relations, as we saw in noting that the differences in form and size might be often directly referred to the unequal resistance in the immediate environment. Where the connective-tissue envelope yields to the pressure of the growing parasite, a diverticulum is formed, so that the protrusions and lobes of the irregular *Echinococcus* are ultimately explicable by the same physical principle as that according to which the external portion of the worm, when in a superficial situation, projects from the surrounding parenchyma, and continually grows further outwards. The point of least resistance determines the direction of this growth, so that *Echinococci* situated near the convex surface of the liver rise towards the thoracic cavity, while those near its lower surface sink down into the abdomen.

The pressure exerted on the bladder-wall and on the neighbouring organs frequently excites a more or less marked reaction. First, inflammation sets in, which is either limited to the *Echinococcus*-cyst, or spreads to the adjacent tissues, and then results in a more or less extensive adhesion of the affected parts. The *Echinococcus*

becomes attached to the adjacent organs, now to the intestine or kidney, now to the diaphragm or abdominal wall.

The inflammation entails further consequences. It leads to ulceration and destruction of the affected parts. The cyst-wall gives way, and the *Echinococcus* protrudes like a hernia to a varying extent. The diverticulum reaches spaces which were previously shut off from the worm. In the one case it is perhaps the abdominal or thoracic cavity which receives them; in the other, it is the intestine or the lumen of a vessel, according to circumstances.

If the diverticulum be but small, and the cavity into which it has penetrated be surrounded by close and resistant walls, so that there is a counterbalancing pressure, then the worm retains for a lengthened period its original character. It fills the cavity, penetrating to an ever-increasing extent. This is most frequently the case with the multilocular *Echinococcus*, whose processes penetrate into the ramifications of the bile-ducts, as well as into the portal vein and lymphatics, and sometimes grow into them in such a way as to suggest that the peculiar form of the *Echinococcus* is determined by the spaces which it occupies.

In such cases the anatomical result is very much what we have above described in the case of *Echinococcus* of the brain, or of the pleural cavity, when it has left its original seat and expanded in the neighbourhood.

But it is not always so. When, owing to the size and extensibility of the newly occupied space, there results a lessening of the resistance to the diverticulum from the cyst, then the latter continually increases, and becomes more distended with fluid and hydatids, until it finally bursts either spontaneously, or in consequence of some external cause, and expels its contents.

This issue is extremely frequent in the larger *Echinococci* of the viscera, which are mostly of the hydatid variety. From Neisser's results we see that of 451 cases observed in the liver, the third part terminated thus. The majority opened either into the alimentary canal (forty-five cases), or, after perforation of the diaphragm,[1] into the bronchi (thirty-one). In sixteen cases each the contents were emptied into the body-cavity and pleural cavity, and a breach through the abdominal wall was equally frequent. The large vessels (veins) and

[1] To the cases of this sort, collected by Davaine (*loc. cit.*, p. 440), I may add a new one observed by Professor Blasius. The preparation is lodged in the Anatomical Museum of the University of Halle, and bears the following label:—"Pulmo et hepar sutoris 40 ann. n. Frauendorf. Inde ex annis 15 ex echinococcis hepatis ægrotus crebris peritonitidis insultibus vexatur, postremis annis echinococcos bile tinctos cum sputis edidit. Pulmonis dextri lobus inferior echinococcus destructus per diaphragma cum ductu hepatico dextri lobi hepatis anastomosin inivit."

also the ureters and bile-ducts (though less frequently, because of their smaller size), are also occasionally the seat of the rupture. In some cases, a twofold rupture is observed in the same *Echinococcus*, usually into intestine and lungs, or more rarely into the intestine and ureter.

Such a rupture is more frequent in the *Echinococci* of the lungs than in those of the liver, so that evacuation often takes place through the bronchial tubes. Among the sixty-eight cases enumerated by Neisser, no fewer than thirty-one had this issue, nine led into the pleural cavity, while the rupture took place into the pulmonary veins, intestine, and through the umbilicus once in the case of each.

Here and there a rupture has been observed in the *Echinococci* of the pelvis, leading either into the body-cavity or to the exterior through the female generative passages, and once (in Sibille's case) through the perinæum.

The prognosis varies in all these cases according to circumstances. First we must take into consideration, besides the intensity and extent of the ulcerative inflammation caused by the rupture, the nature of the affected organ. The more sensitive it is to external influence the more unfavourable is the situation; in many instances, *e.g.*, where the contents are poured into the pleural or abdominal cavities, the case is almost hopeless.

In these cases the evacuation is followed by a violent inflammation of the peritoneum or of the pleura, and this is usually rapidly succeeded by death. Where the inflammation has a less serious character this is probably due to the small quantity of the emptied matter, and to its condition. Of importance, therefore, in this connection are the differences in the number, size, &c. of the daughter-bladders.

The state of the case is much more favourable when the rupture has been effected directly to the exterior through the abdominal walls or the intercostal spaces. This is especially the case when the fistula is short, and when the emptying of the daughter-bladders presents little difficulty. Under such circumstances the rupture leads not unfrequently to a perfect recovery, so that of late years it has been sometimes artificially produced (by caustic paste according to Récamier) in order to effect a radical cure. Of course there are also cases in which the rupture, whether natural or artificial, may prove fatal in consequence of peritonitis, or of long-continued suppuration and exhaustion ensuing.

When the *Echinococci* (even if *E. hydatidosus*) open into the bronchiæ, or the intestine, recovery is usually only a question of time. This is specially true in the case of rupture into the intestine, for

among the forty-three such cases cited by Neisser no fewer than thirty-seven were cured, while in the cases where the contents were evacuated by expectoration, only about three-fourths (twenty-three out of thirty-one) recovered. From the intestine the expulsion of the bladder contents is usually effected *per anum*, and only in the case of ruptures situated high up *per os*. The expulsion is sometimes so favourably accomplished that the hydatids reach the exterior uninjured. Davaine mentions the case of a woman in Paris who was thus suspected of laying eggs. In the majority of cases merely membranous shreds are voided, and their true nature is sometimes recognisable only by the help of the microscope.

Besides the above-named organs, the blood-vessels sometimes receive the contents of the burst *Echinococcus*. This may happen, for example, if the parasite have been developed in the cardiac muscles and burst through the endocardium after a longer or shorter period of inflammation. It may also occur in the liver or lungs, in which cases the large vessels, and especially the veins, are affected by the worm exactly as were the hepatic ducts or bronchiæ. On the whole, such cases are rare, and happily so, since they are almost always fatal either gradually or more suddenly (by thrombosis). Professor Luschka had the goodness to tell me of an interesting case of this sort, which I note the more readily, since there are but few such observations on record. It concerned a woman forty-five years old, who died suddenly with symptoms of asphyxia, and yet without apparent cause. On dissection the cause was revealed. In the region of the posterior border of the liver there was an *Echinococcus* about the size of a child's head, which in the fossa venæ cavæ had broken through the wall of that vessel, and there liberated its contents. The daughter-bladders had reached the right chamber of the heart, and thence also the pulmonary arteries, where they had induced an embolism which rapidly caused death. When the obstruction of the pulmonary arteries is incomplete, then, instead of sudden death, a more protracted disease ensues, that has essentially the same symptoms as stenosis of the pulmonary artery, and, like it, is accompanied by dilatation and hypertrophy of the right heart.

The situation is very different when the daughter-bladders pass through the pulmonary vein into the current of the aorta, and thence into the peripheral vessels; the result being that the portions robbed of their blood supply mortify.

The phenomena evoked by *Echinococcus* in brain or eye are like those occasioned by *Cysticercus cellulosæ*. Their intensity is, indeed, greater, but that is sufficiently explained by the more prolonged and more vigorous growth of the worm. In the interior of the eye it has

been observed only a few times, and always associated with complete loss of sight. The *Echinococci* in the brain are still more serious, and have always, after a longer or shorter period, a fatal issue.[1] As a rule the disease is first manifested by violent and continual pain in the head and joints, not unfrequently as a decided neuralgia, accompanied by giddiness, fainting, and vomiting. Sooner or later attacks of cramp begin to occur with varying frequency, and sometimes of a decidedly epileptic character. The sensory and cerebral functions are gradually increasingly disturbed, voluntary movement is suspended, and death supervenes sometimes after apoplectic ruptures and softening round about the parasite.

Those in the muscles and peripheral organs (thorax, salivary glands, oral cavity, &c.) are on the contrary almost harmless. They only act as hindrances, impeding the functions, and are usually readily removed.

Since these superficial *Echinococci* are on the whole but rare, our judgment as to the clinical importance of the worm can hardly be thereby modified. We are forced to regard it as one of the most dangerous parasites infesting man, dangerous because of the disease it originates, dangerous also because we are in many cases, and these the most serious, quite helpless against it. Since we can do so little to dislodge this unwelcome guest, it is a weighty fact that Nature herself sometimes sets a limit to the destructive work. As we have noted, it by no means rarely happens that the *Echinococcus* dies either at an earlier or later stage of development. The cause of this phenomenon has usually been sought in certain conditions of the surrounding cyst. A change is to be observed affecting the granular cellular layer over-lying the bladder. This is at first not unlike a serous coating, but it begins to become loose and turbid. It frequently changes into a creamy or caseous mass,[2] accumulating ever more and more round the bladder-worm.[3] The latter seems for a while hardly in any wise altered. But on closer examination one is convinced that the parenchyma is softened and has undergone fatty degeneration, that at some points it has been separated from the cuticle, and that the heads swim about freely in the fluid, and present a more or less altered appearance. At a later stage this fluid is exuded. It collects round about the bladder-worm, and forms a thick mass of a glue or honey-like character, being more or less mixed with the granular substance of the cyst-wall. The bladder collapses in consequence of the loss of the fluid. It shrivels

[1] Westphal's case of an intracranial *Echinococcus*, from which the patient recovered (*Berliner klin. Wochenschr.*, No. 18, 1873), is quite unique.

[2] See the above cited observations of Kuhn, "Rech. sur les acéphalocystes," and Cruveilhier, "Anat. path. gén.," t. iii., p. 550.

[3] I have seen livers of cattle in which all the *Echinococci* were thus changed, so that one was compelled to look for the cause in the state of the affected organ.

more and more, loses its former pellucid appearance, and becomes an indiarubber-like substance, which finally (though perhaps after a considerable time) degenerates into an amorphous detritus. The tumour, of course, decreases in size as the fluid is absorbed. This may take place so thoroughly that only a small knot remains where there formerly existed a conspicuous *Echinococcus.*

Sometimes during this change a large quantity of lime, especially of the carbonate, is deposited in the former granular layer, so that the latter can not only be removed from the substance of the surrounding organ as a connected mass, but even presents considerable resistance to the knife. Berthold examined the calcareous shell of such an *Echinococcus* from the lung of an old dromedary, and distinguished on section two layers, one over the other. Of these, the outer and firmer was composed mostly of phosphate; the inner, on the other hand, of carbonate of lime. In the latter there were here and there massive deposits of lime of a distinctly crystalline character.[1]

The changes here described have been in part already observed by the older anatomists, though their true nature was not recognised.[2] Starting from the supposition that the *Echinococci* were of the nature of tumours, it was thought that transitions might be traced from the hydatids sometimes into tubercles (Morgagni), sometimes also into atheromata, steatomata, melicerida (Ruysch). Even the demonstration that the *Echinococci* were animals allied to the bladder-worms has not quite dismissed the old idea, for even in 1819 the attempt was made to deduce from them not only tubercular deposits, but also scirrhus and other neoplastic formations.[3]

It requires no special mention that the many and serious disturbances induced by the *Echinococcus* suggested their association with dangerous tumours; and that all the more, since the life-history and development of the parasite exhibits various phases, the zoological nature of which is difficult to determine. I recall, for instance, the existence of the so-called "secondary" hydatids, and further, that the power of movement, which was usually regarded as one of the most important attributes of animal life, seemed here wholly absent.

The medical public has but slowly and reluctantly acknowledged the true nature of this parasite; and even when no one doubted that the *Echinococcus*, and particularly the hydatid *Echinococcus*, was in

[1] *Göttingische gelehrte Anzeigen*, p. 1975, 1837.

[2] See Küchenmeister's results, *Deutsh. Archiv f. Gesch. d. Med.*, Bd. ii. u. iii.

[3] Baron, "An Enquiry illustrating the Nature of Tuberculated Accretions and the Origin of Tubercles:" London, 1819; and a subsequent paper, "Illustrations of the Enquiry respecting Tuberculous Diseases:" London, 1822. One must note that Baron used "hydatid" in the wide sense of the old physicians, and made it include more than the *Echinococci.*

truth an animal, and the young stage of a tape-worm, yet the multilocular form was still regarded as a tumour. Now, however, this error has been dissipated, and our knowledge of this important parasite has attained a fairly satisfactory completeness and certainty.

Division II.—*Ordinary Tape-Worms* (*Cystoidei*).

As we have already noted (p. 360 and p. 400), this group includes all those *Tæniæ* which are not cystic tape-worms. They do not, however, form a single well-defined group, but rather include many diverse types. They are distinguished from the cystic tape-worms by the manner of their development, *i.e.*, by the absence of a proper bladder-worm stage. They possess, indeed, usually a larval stage somewhat resembling the bladder-worm, but this is so small, and its bladder is so little developed, that in spite of the resemblance the term "bladder-worm" is hardly applicable. Strictly speaking, the embryonic body of this young stage (Cysticercoid) cannot be regarded as the bladder, since it is solid, and has not that accumulated fluid which suggested the theory that the true bladder-worm was a dropsical degeneration. The "bladder" is, however, usually distinctly marked off from the

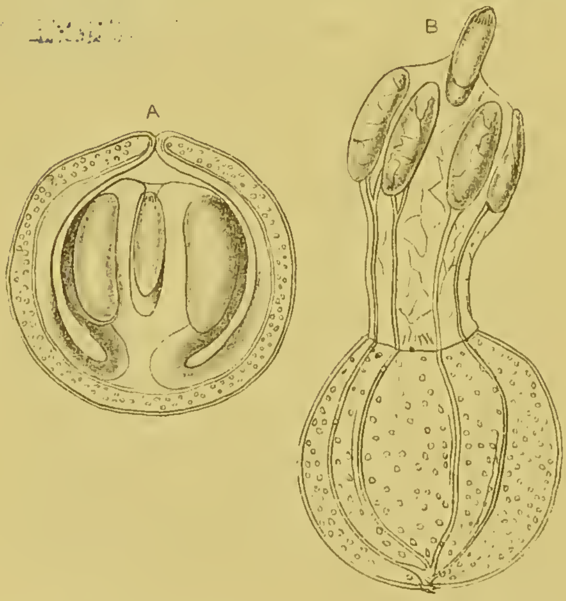


Fig. 336.—*Cysticercus arionis*, with (*A*) retracted and (*B*) evaginated head. (× 50.)

Fig. 337.—*Cysticercus glomeridis*, after Villot. (× 50.)

rest of the tape-worm body, and is, even in the extended state, recognisable as a distinct structure. It possesses a more or less firm, some-

times finely streaked cuticle, on which in some cases the embryonic hooks still lie, and under which there is a finely cellular parenchyma, often penetrated by numerous fat globules. Since it is contractile, it probably contains muscle-fibres. Calcareous corpuscles are, it seems, found only in the appended head-process. Similarly, the ramifications of the vessels appear to be exclusively confined to the latter, although the longitudinal stems are seen to traverse the bladder, and to open by a foramen at the lower end.

In contrast to these common forms of Cysticercoid, there are others in which the sac-like outer body in appearance and structure resembles a simple continuation of the head-bearing anterior body, to which it stands almost in the same relation as the posterior portion of the *Echinococcus*-head to the anterior end, which bears the attaching apparatus. We have already (p. 364) noticed this formation, especially in the Cysticercoids of *Tænia cucumerina*, and have attempted to show that this outer body was, in spite of its divergent structure, still nothing but the caudal bladder, *i.e.*, the first developmental product of the six-hooked embryo. The morphological individuality (p. 386) has indeed been lost; head and caudal bladder appear as a unit, whose development presents rather the appearance of a metamorphosis than of an alternation of generations.

FIG. 338.—Cysticercoid of *Tænia cucumerina*. (× 60.)

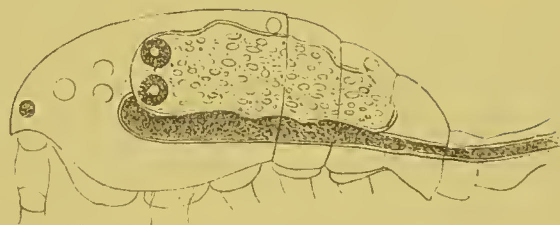


FIG. 339.—Young form of *Tænia torulosa* (?) in *Cyclops serrulatus*, after Gruber. (× 25.)

This is perhaps yet more distinct in the Cysticercoids from the *Cyclops* discovered by Gruber, where the head is always protruded, instead of being retracted into the posterior body, the characteristic form of the bladder-worm being thus disguised.

As in the development of the caudal bladder, so in the position of the head there are manifold differences, and that even when we leave those with free head out of account, and confine ourselves to those species in which the head is retracted into the body.

Among these there are first of all some species in which the head has exactly the same position that we have described in the cystic tape-worms as primary and normal. The head is completely invaginated, so that the subsequent external surface forms the inner lining of a pouch hanging down as a process in the axis of the bladder. The hook-apparatus is found at the deepest part of the pouch. This is not only the case in the young stage of *Tænia cucumerina* (Fig. 338), which in the structure of its posterior body is especially connected with the Cysticercoids of the *Cyclops;* but so it is also in the so-called *Gyporhynchus* of the tench (p. 364), which possesses a distinct caudal bladder, although its head-end is sometimes protruded therefrom, and used for creeping about in the host, just as do the larvæ of the *Tænia* found in *Cyclops.* This slight difference is noticeable, that in the Cysticercoids there is never the development of a vermiform body intercalated as a long neck between head and bladder, as is seen so frequently, and often so strikingly, in the true *Cysticerci,* especially in *C. fasciolaris.*

If our conception of the developmental history of the Cysticercoids be correct (see p. 362), then the head has always at first the position here described. The attaching apparatus is of course always formed inside a bladder (the enlarged six-hooked embryo), the first rudiment of the head appears as a hollow bud, which often at an early stage exhibits an elevation at its base, which grows ever further outwards until the head attains its final structure, and shows inside the distended sac-like neck exactly the subsequent position of the tape-worm head. Since, so far as we know, it is especially the species with extended rostellum, *e.g., Cysticercus arionis* (Fig. 336), which exhibit this formation, we may suppose that the elevation of the head is determined by the outgrowth of this structure, and that the position of the head above noted has therefore only a secondary importance.

As to the development of the Cysticercoids, I must refer to what I have already said (pp. 360-368). This may again be specially mentioned, that there are among them some forms which appear as many-headed and racemose bladder-worms analogous to *Cœnurus* and *Echinococcus.*

As yet we know but few Cysticercoids, so few that one sometimes still hears the doubt expressed whether all the hundreds of known *Tæniæ* have, indeed, passed through a Cysticercoid stage. We have already referred to the difficulties attending the search for Cysticercoids (p. 379, Note), and can only further answer that until the demonstration of a direct development our positive experimental results must be held as decisive, and they all prove the existence of an intermediate Cysticercoid stage.

If we leave out of account the *Cysticerci* (p. 343) found in the parenchymatous tissue of birds (*Piestocystis*, Dies.), which in many respects connect the ordinary bladder-worms with those now under discussion, we may say that only cold-blooded animals harbour the Cysticercoids. The majority occur in the Arthropoda, and especially in insects, but also in fish, worms, and snails. In marine animals the Cysticercoids are extremely rare; we know as yet only a single form (from a Pteropod), but this readily harmonises with the fact that the adult Tæniadæ occur very rarely in marine animals. The great majority inhabit terrestrial and fresh water animals, especially birds and mammals, and chiefly those which feed on insects and vegetable food. Both classes of animals get their parasites from their food, the one by directly eating the intermediate hosts, the other by the accidental swallowing of the same. Man, mostly in his youth, may be infected in either of these ways.

We have already noted the numerous variations in the external appearance and internal structure of the Cysticercoid tape-worms. We find among them species with many, and species with few joints, some small and short, others long and broad, some, indeed, the longest tape-worms we know,[1] some armed, others hookless. In many of the latter the head is as large as, or even larger than, that of *Tænia saginata*, while others, especially among the armed forms, are less developed in this respect. Similarly the hooks show in number, size, and arrangement the most manifold variations, much more striking than in the cystic worms. Generally the development of the attaching apparatus is less powerful. With, too, this agrees the formation of the rostellum, whose muscular walls enclose a spacious cavity, which is all the more striking since the early lenticular form has been exchanged for an ovoid or cylindrical one. In the last instance the apex often forms on the protrusion of the rostellum a more or less long and lank proboscidiform projection.

The adult proglottides are usually short, much shorter, indeed, than they are broad, and are more firmly connected with one another than in the cystic tape-worms, so that in expulsion long stretches rather than single joints are set free. The uterus has usually the form of a wide cavity with more or less numerous boss-like or pouch-like diverticula. Here and there we find the dendritic ramifications of the larger cystic tape-worms, with this difference, however, that the main stem has, in correspondence with the shape of the joints, a transverse instead of a longitudinal course. In other cases the diverticula become isolated as they are filled with eggs

[1] The *Tænia expansa* of the ruminants is sometimes, according to Göze and others, over 100 feet long. It has generative pores on both sides like *Dipylidium*.

and form small independent brood-pouches, filling the middle layer of the joint, varying in number and arrangement. The structure of the germ-producing organs exhibits also numerous variations, which are in part so fundamental and characteristic that various attempts have been made to utilise them for systematic purposes. We have already noted many of these peculiarities, but we may shortly revert to them. Sometimes the female reproductive organs recall exactly the structure of the cystic tape-worms, while the testes are but sparsely developed, being, indeed, sometimes reduced to two or three. On the other hand, the male and female spermatic reservoirs and the cirrhus often attain a considerable size. The generative openings usually lie all on the same margin, but are occasionally found on both sides. The eggs have besides the thin light-brown shell, and the very constantly persistent vitelline membrane, not unfrequently a third middle envelope. Where the uterine cavity is broken up into distinct brood-pouches, as is the case in the Cystoidei of man, then all the contained eggs of the latter are during the formation of the embryos united into a single mass, which is in some respects comparable with the cocoon of the leech or earth-worm. The embryonic hooks are often of considerable size, and are in some cases larger than the hooks of the adult worms.

We cannot yet determine with certainty how many human tape-worms belong to this group. As yet we only know four, but these have all been lately discovered, and the number will doubtless be yet increased. This is the more probable, since, with one exception, these worms belong to foreign countries, where helminthology has been little prosecuted, and where the mode of life and nutrition of the inhabitants is in many respects favourable to the importation of Cysticercoids.

To all appearance, then, the number of cysticercoid *Tæniæ* in man is larger than that of the cystic tape-worms; but none of the former can be compared to the latter in distribution, frequency, or clinical importance. It seems even doubtful whether any one of them is peculiar to man. The species indigenous in our country,[1] *Tænia cucumerina*, is certainly not, for it is usually found in the dog and cat, and only occasionally in children.

According to their natural relationship these worms belong to various groups, the members of which are probably in every case confined to the Mammalia.

[1] We must leave it as undecided whether the smooth-shelled *Tænia*-eggs found by Ransom in the fæces of a child belong to a second European species (*Medical Times*, vol. x., p. 598, 1856). The same must be said of Heller's report, according to which the Erlangen Pathological Institute contains a *Tænia* as yet unidentified, which was voided by a child (Ziemssen's "Handb. d. sp. Path. u. Ther.," Bd. vii., p. 560); Eng. transl., vol. vii., p. 670.

GROUP A. *Head small, with a single circle of small hooks, seated on an ovoid rostellum. Joints short and broad, even when mature. Generative openings on one side, testes few, a small receptaculum on the short vagina. Cirrhus-pouch poorly developed. The uterus, a wide cavity extending across the whole joint, and with irregular diverticula. The eggs have two smooth shells, and contain an embryo with somewhat large hooks.*

Subgenus Hymenolepis, Weinland.

The various species are usually short, and are most commonly found in insectivorous animals.

Other related forms, usually from herbivorous animals, are specially distinguished by the absence of hooks, and by the considerable length of the jointed body.

Tænia nana, von Siebold.

Von Siebold und Bilharz, "Zur Helminthographia humana,' *Zeitschr. f. wiss. Zool.*, Bd. iv., p. 64, Tab. v., Fig. 18.

A small tape-worm, from 12 *to* 20 *mm. long, and with a maximum breadth of* 0·5 *mm. In the anterior third the body is thread-like, but posteriorly it enlarges somewhat quickly, so that the last third has an almost uniform breadth. The spherical head has a diameter of about* 0·3 *mm., and bears, besides the four round suckers* (0·1 *mm.*), *a rostellum of* 0·06 *mm., whose anterior truncated portion has a single circle of from twenty-two to twenty-eight extremely small hooks. The number of segments amounts to* 150-170, *of which the last contain thirty or more ripe eggs. The length of the joints is insignificant, and at the posterior end of the worm hardly amounts to quarter of the breadth. The uterus corresponds in form to the joints, and contains numerous eggs of* 0·04 *mm. in diameter, with embryos of* 0·023 *mm.*

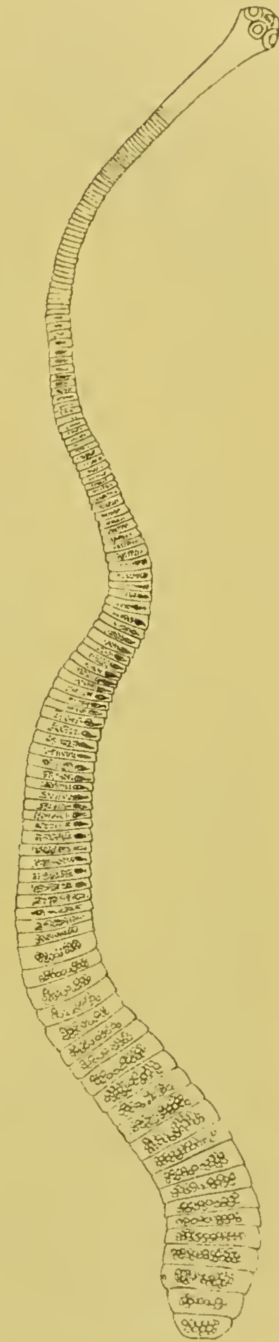


FIG. 340.—*Tænia nana.* (× 18.)

The tape-worm which is here shortly described was discovered by Bilharz in Egypt, and although hitherto observed only in a single

case of a boy who had died from meningitis, it was in this instance found in countless numbers in the duodenum.[1] We owe our knowledge of it to v. Siebold, who has published the communications made to him by Bilharz, along with a drawing of the anterior end of the body, in the above-quoted memoir. But as we have already mentioned in another connection, the account is unfortunately very insufficient, so that it would be difficult to recognise the worm from it. All the more do I rejoice that in the above diagnosis, and the following statements, I am able to offer the results of an independent investigation. The specimens which were placed at my disposal came from Bilharz himself. I received them through the kindness of Professor Claus from Dr. Markusen, and partly also from Professor Welcker in Halle, who most willingly sent me a number of duplicates from the collection of Egyptian Helminths presented by Bilharz to the Anatomical Museum in Halle.

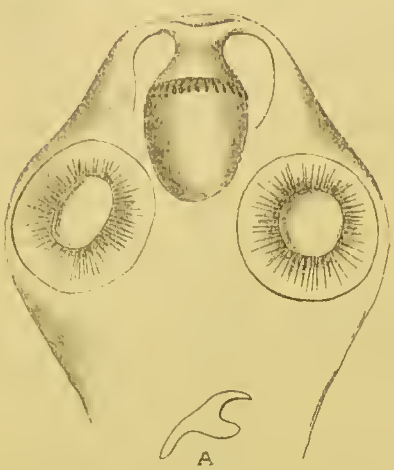


FIG. 341.—Head of *Tænia nana*, with retracted rostellum (× 100). (*A.*) An isolated hook (× 600).

In the largest of my specimens the length of the worm is 15 mm. (Bilharz mentions one of six and the other of ten lines in length.) The head is almost one-half larger than the adjacent neck, whose separate joints can only be distinguished at some distance. I always found the rostellum in a retracted condition. The hooks consist, just as in the cystic tape-worms, of a claw and two roots, of which the anterior one is very thick, and the posterior more slender, as is also often the case in other Cysticercoid *Tæniæ*.[2] The claw is slender, and has a sharp point, by which it is easily distinguished from the equally long anterior root.[3] All the hooks are of exactly the same

[1] Spooner indeed thinks that he has observed *T. nana* in America (*Amer. Journ. Med. Sci.*, Jan. 1873), and that in a young man, who, in consequence of the worm, exhibited symptoms quite similar to those caused by the presence of a large-jointed tape-worm. But the diagnosis appears somewhat uncertain and suspicious. Perhaps the parasite belonged to the following species, which, as we shall see, is indigenous to America. [Hellich has recently obtained *T. nana* in numbers from a girl seven years of age in Belgrade. I have had the opportunity of examining some of these specimens, and thus not only of confirming the diagnosis, but also of correcting some of my former statements regarding the species.—R. L.]

[2] Bilharz's expression "hamuli bifidi" (v. Siebold, *loc. cit.*) is probably due to his erroneous interpretation of this anterior root-process as a second claw.

[3] This is the case not only in the related tape-worms of our mice and shrews, but also in Stein's Cysticercoid from *Tenebrio*, and in a number of *Tæniæ* from birds; regarding the latter see Krabbe, "Bidrag til Kundskab om Fuglenes Bandelorme," Tab. viii., ix., Kjöbenhavn, 1869.

form and size. The latter is, however, very insignificant, and is even less than in *Tænia echinococcus*, for according to my measurements the total length does not amount to more than 0·018 mm. The distance between the two roots is 0·015 mm., and that between the end of the anterior root and the point of the claw 0·0076 mm.[1]

Soon after the appearance of the segmentation one notices in the centre of the individual segments a bilobed accumulation of dark granules, which become more abundant and distinct posteriorly, and

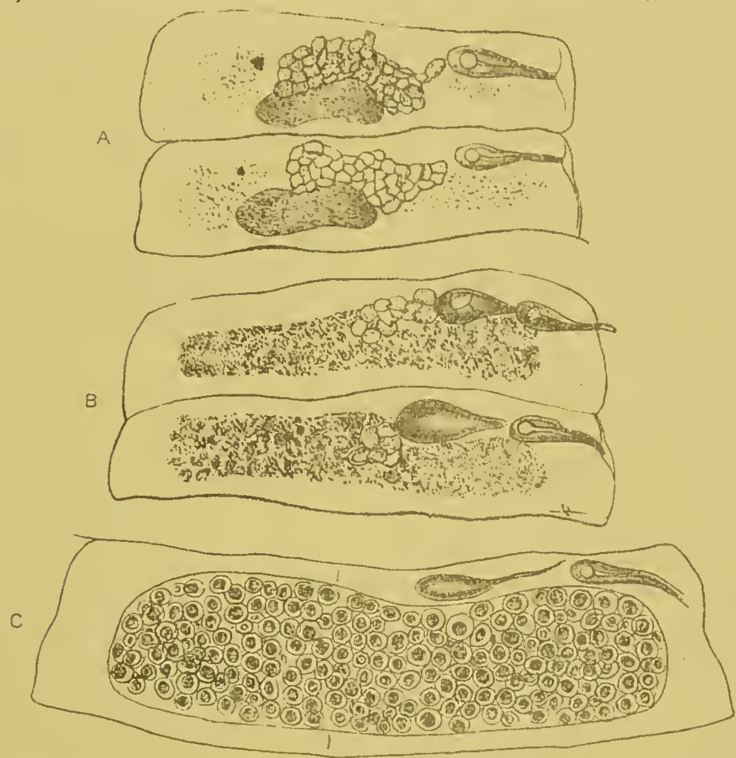


FIG. 342.—Proglottides of *Tænia nana* (× 100). (*A.*) With female genital glands; (*B.*) With formation of eggs commencing; (*C.*) In mature condition.

gradually assume more definite forms. In addition to these there appears after a time a sharply defined club-shaped organ, which, near the anterior border, runs through the joint in a transverse direction, and sometimes projects with its rounded and thickened end as far as the middle of the latter. In the interior of this club there is a cylindrical passage, the end of which is enlarged into a spherical cavity.

There can be no doubt that this structure is part of the male organs, and performs the functions of a cirrhus or cirrhus-pouch; indeed, I have sometimes seen its point protruding for a short distance beyond the sharp border of the joint.

[1] [In the drawing (Fig. 341, *A*) the posterior root is represented as too short; it should be twice as long.—R. L.]

Further, the nearer the joints approach the middle of the body, the more does the above-mentioned granular mass assume the appearance of a number of closely packed lobes. The latter are grouped together into an irregular, two-lobed figure, the parts of which are distributed over the two lateral portions of the joint. Close behind the mass there is observed another structure of a more finely granular nature which I have recognised as the yolk-gland, while the organ lying above it represents the two ovaries. The testes are three in number, and situated near the posterior border of the segment.

In the joints of the middle of the body a new structure appears behind the cirrhus-pouch, which, on account of the increasing breadth of the segments, has in the meantime drawn nearer and nearer to the side. It is a body of a pear-like form, which has an almost fatty and shining appearance, and at first sight might be interpreted as a vesicula seminalis. And, indeed, the contents of this body consist of seminal filaments, closely aggregated into an almost homogeneous mass; nevertheless I am quite convinced by the examination, not only of *Tænia nana*, but also of the related forms[1] that it is not a vesicula seminalis, but a receptaculum seminis. It is filled by means of a short vagina, which opens beside rather than under the cirrhus-pouch, and consequently can but rarely be observed with perfect distinctness. As the filling proceeds, the female genital organs become gradually more shrivelled and blanched, while, on the other hand, the uterus becomes distended with numerous corpuscles, which can soon after be recognised as eggs. The more these develop, the more does the receptacle lose its former refractive power. It becomes paler and smaller, and, along with the cirrhus-pouch, gradually retires in an anterior direction before the pressure of the uterus, until it comes to lie close to the anterior border, where it is easily overlooked.

I must contradict the statement of Bilharz, that the eggs of *Tænia nana* possess a "thick and yellowish" shell. As I have remarked above, I can clearly distinguish two thin and clear, but somewhat firm egg-shells, which are widely separated from each other. The six hooks could be but rarely perceived in the coarsely granular embryonic substance, but in several instances they were discovered in the form of little rods, 0·0095 mm. in length, with bent, sickle-shaped points.

FIG. 343.—Ripe egg of *Tænia nana*, with embryo. (× 250.)

Only a few calcareous corpuscles of insignificant size were distributed through the parenchyma of the body.

[1] If taken in connection with the foregoing observations by Stieda, Feuereisen, and Steudener, my communications supply a somewhat complete picture of the structure of the

Regarding the origin of the worm, we are at present unable to give any authoritative decision, and we shall therefore content ourselves with the supposition that, as in the most nearly related species, the worm passes its youth as a Cysticercoid in some insect or snail. The large numbers of the worms by no means contradict this supposition, since, in order to account for them, there is no need of assuming a repeated transmission; on the contrary, they may be quite sufficiently explained by the observations of Villot regarding the Cysticercoids of *Glomeris* (p. 367), which, like the Cysticercoids of Stein, from *Tenebrio*, belong to this group.

Küchenmeister's attempt to rank the worm along with *Tænia echinococcus* is altogether excluded by its organization.

Tænia flavo-punctata, Weinland.

Weinland, "Essay on the Tape-Worms of Man," Cambridge, U.S.A., 1858, p. 49.
Weinland, "Beschreibung zweier neuer Tænioiden aus dem Menschen," *Nova Acta Acad. Cæs. Leop.-Carol.*, t. xxviii., pp. 8-12, tab. iv., 1861.

This tape-worm, which has hitherto been only once observed[1] *and described, attains the length of about a foot. The anterior half of the body consists of unripe joints,* 0·2 *to* 0·5 *mm. long, and from* 1 *to* 1·25 *mm. broad, each of which exhibits posteriorly a central yellow spot of somewhat large size. This is the distended receptaculum seminis (Weinland's testis). In the second half the joints attain a length of* 1 *mm., and a breadth of* 2 *to* 2·3 *mm. They have lost the yellow spot, and owing to the abundant development of eggs, have assumed instead a brownish-grey colour. The eggs are surrounded by a smooth double envelope, and are about* 0·06 *mm. in size. The uterus is a simple wide cavity, which occupies almost the whole segment. The form of the hindermost joints is trapezoidal, with a more or less narrow anterior border, or sometimes almost triangular. The nature of the head is unknown,* (?) *but it was probably armed with a single row of small hooks.*[2]

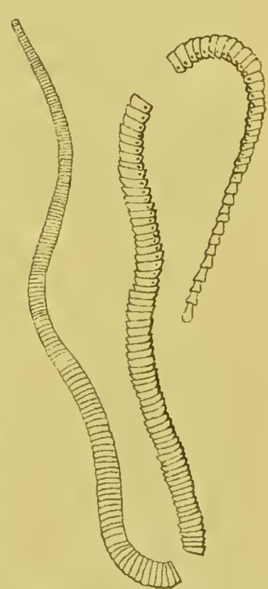


FIG. 344.—*Tænia flavo-punctata*, after Weinland (nat. size).

sexual organs of *Tænia nana*. In most points the reconstruction would closely correspond with the drawing given by Feuereisen of the sexual apparatus of *Tænia setigera* (see Fig. 160).

[1] [Since the above was written, this worm has been observed in America by Leidy (*Proc. Acad. Nat. Sci. Philad.*, p. 137, 1884), and the same or a closely allied species in North Italy by Parona (*Giorn. R. Acad. Med. Torino*, fasc. 2, 1884); on both occasions the host was a child.—R. L.]

[2] [The worm observed by Parona had a club-shaped head, without hooks or rostellum. —R. L.]

I borrow the foregoing diagnosis (with the exception of some insignificant details) from the description given by Weinland (*loc. cit.*) of some worms bequeathed by Dr. Ezra Palmer to the Museum of the Society for Medical Improvement in Boston, Mass. The specimens had been determined as *Bothriocephalus*, and preserved in spirit. The six longer specimens, investigated by Weinland, measured altogether about three feet, and were voided by an otherwise healthy child, that had been weaned about six months before, without any suspicion being entertained of the presence of the parasite.

At my request, Dr. Weinland was kind enough to send me for investigation about an inch of this tape-worm. This portion was from the middle of the worm, and exhibited hardly anything else than a countless number of eggs, which filled the whole interior of the joints, with the exception of the clear, thin, enveloping wall. The only thing else that could be distinguished was a clear, club-shaped organ, occupying a transverse position upon the anterior border of the joints, and the rounded end of which extended about as far as the middle line of the worm, but the other was continued into a thin canal, which ran towards the adjacent lateral border, and there terminated in a distinct opening. The analogy of *Tænia nana* and the related forms enabled me to recognise in this structure the vagina with the large receptaculum seminis. The cirrhus-pouch eluded observation, but whether on account of the opacity of the preparation, or because of its complete disappearance, I cannot decide; very probably it is of small size. There are, moreover, so many resemblances between Weinland's species and *Tænia nana*, not only in regard to the formation of the vagina, but in other respects, that I have not the slightest doubt of their near relationship. The formation of the eggs is also the same, with the exception, indeed, of the difference in size, which is in favour of the North American species. Weinland certainly describes three egg-membranes in his species, but, in spite of careful investigation, I have been unable to distinguish more than two, which are identical with the inner and outer ones of Weinland. The thin, middle membrane, which is said to cling closely to the former, and to be always wrinkled in the preserved specimens, I have never

FIG. 345.—Ripe proglottides of *Tænia flavo-punctata*, one barren. (× 40.)

been able to find. Indeed, I am almost inclined to think that Weinland has been misled by the coagulation of the not unfrequently granular mass, lying between the widely separated inner and outer shells. The embryo measures almost 0·03 mm., and after the application of alkalis distinctly exhibits its six hooks (0·017 mm. in length).

Among the segments which I examined there was one which, even on cursory observation, attracted attention by its pale appearance and small size, and especially by its narrowness. On microscopic examination it proved to be without eggs, and had apparently, from some unknown cause, never formed any. The receptaculum, with its efferent canal, was more distinct than in the fertile proglottides, and also of a larger size, unquestionably because the material had not been expended otherwise. If I remember aright, the friendly donor himself called my attention to this joint, with the remark that he had repeatedly observed similar sterile proglottides in his *Tænia flavo-punctata.*[1]

The calcareous corpuscles are in this species also small and scanty.

GROUP B. *As in* Hymenolepis, *the sexual apertures are unilateral, and the eggs provided with two smooth envelopes, and, instead of being isolated, enclosed in a group within a firm enveloping substance, which is continued exteriorly by a felt-like fibrous tissue. Head ?*

Subgenus —— ?

Tænia Madagascariensis, Davaine.

Davaine, "Note sur une nouvelle espèce de ténia, recueillie à Mayotte," *Archives de médecine navale*, t. xiii., 1870.

Davaine, "Traité des Entozoaires," second edition, p. 922 ; or *Mém. Soc. biol.*, 1870.

A Tænia *of probably about* 8 *cm. in length, and with about* 100 *somewhat broad joints, which are at first short, but gradually assume an almost square form, measuring in length and breadth about* 2·6 *mm. In the interior of these joints there are a large number of small bodies of oval form* (0·9 *mm. long and* 0·6 *mm. broad*), *which are arranged in transverse rows, alternating with each other, but without touching at any point. Their number in each proglottis amounts to from* 120 *to* 150. *These are not eggs, as might have been supposed, but balls of eggs, covered externally by a spongy substance of somewhat considerable thickness, in the form of a clear sphere* (*of* 0·5 *or* 0·3 *mm.*). *The eggs themselves always measure* 0·04 *mm.* (*the inner egg-shell* 0·02, *and the embryo* 0·015 *mm.*), *and the number found in each ball is about* 300 *to* 400. *In favourable*

[1] In two communications which have appeared since these words were written (*Nova Acta Acad. Cæs. Leop.-Carol., loc. cit.*) Weinland has himself described this abnormality. Similar sterile joints are occasionally found in other tape-worms.

objects the embryonic hooks appear in the form of fine rods. Regarding the structure of the head and the anterior part of the body unfortunately nothing is known. The smallest joints hitherto observed had a breadth of 2·2, *and a length of* 0·8 *mm.*

We owe the discovery of this worm to Dr. Grenet, head of the French Medical Department in Mayotte, an island on the coast of Madagascar, who expelled it by means of castor-oil from a boy of sixteen months old, and also from a girl two years of age, who had settled in the island only two months before. In both cases the children were suddenly and without any assignable cause attacked with convulsions, which ceased after the use of the anthelminthic. The first patient voided, in consequence of the latter, no fewer than nine, and the other two worms, which unfortunately have only reached Europe in fragments. The largest of these, which was given to Davaine for investigation, contained seventy-five segments. Two other shorter ones exhibited seventeen and eighteen ; and there were further three pieces with two joints each. All of these originated from the first of the two young patients, while from the second there was only received one chain with fifteen ripe proglottides. According to Grenet, the latter possess, in their isolated state, great contractility, and crawl about nimbly upon the fæces, with pronounced changes of form.

What Davaine has communicated regarding the reproductive organs of this species shows that, except as regards the egg-capsules, they essentially correspond with the ordinary forms. The most anterior segments exhibit no recognisable reproductive organs, being as yet sexually undifferentiated (" neutre") ; and the succeeding ones have at first their male organs chiefly developed. The vas deferens and penis could be distinctly observed. The letter is described as a smooth, short, and somewhat stout cylinder (with a diameter of 0·025 mm.) protruding as much as 0·04 mm. out of an opening situated in the centre of one of the lateral borders. The vagina, whose course can be distinctly followed, also terminates as usual in this opening. As we have already mentioned, in giving the characters of the group, the pores are all found on the same lateral border.

The feature which is most characteristic of this worm, and which obviates any doubt as to its specific nature, is, as we also previously observed, the structure and nature of the egg-balls. To the naked eye the latter appear in the form of small points, which become visible as soon as the proglottides are 1 mm. in length. From the structure which they exhibit when placed under the microscope, Grenet has compared them to the cocoons of the leech. Since we have learned

from Davaine that these bodies are not separate eggs, as Grenet supposed, but masses of eggs, which are embedded in and enveloped by a common cementing substance of a firm (apparently chitinous) nature, this comparison is all the more apt; and, moreover, the cementing substance, just as in the leech, is continued externally into a fibrous tissue, the principal stems of which assume a radial direction, frequently anastomosing and uniting to form a spongy coating. Between the ramifications there are a few calcareous corpuscles, which are indeed sparsely distributed over the whole parenchyma of the body.

In some respects this spongy coating recalls the border of rods in the egg-shell of the cystic tape-worms. Like the latter, it increases the vitality of the egg, and probably also serves to preserve it from desiccation.

GROUP C. *The proglottides have two peripheral sexual openings opposite to each other, leading to a male and female efferent apparatus, the latter of which possesses, in addition to the receptaculum, a special germ-gland. The proboscides are oval or spherical, and are provided with a number of rows of small hooks, which, instead of roots, have a discoidal base. After the development of the embryo, the eggs become cemented together into rather large groups.*

Subgenus Dipylidium, Leuckart.

FIG. 346.—Head of *Tænia cucumerina*, with rostellum and hooks, in different stages of contraction. (× 140.)

A small group of tape-worms, which, according to the definition just given, includes only a single species parasitic in the cat and the dog, but which would be considerably increased were we to regard only the presence of two peripheral pori.

Tænia cucumerina, Rudolphi.

(Incl. Tænia elliptica, Batsch.)

In a ripe condition has usually a length of 18 *to* 25 *cm., and in the posterior joints a breadth of* 1·5 *to* 2 *mm. The anterior end of the*

body is thin (0·15 *mm.*) *and thread-like, and provided with a head, in diameter about twice as much. If the proboscis be extended, it forms upon the apex of the head a club-shaped projection, usually short and rounded,* 0·1 *mm. in diameter. The total number of the hooks, which surround the extremity of the rostellum in four irregular rows, is about* 60, *and of these half belong to the lowest row, which contains the smallest hooks* (*only about* 0·0057 *mm. in height, and with a basal disc of the same size*). *The largest hooks are* 0·015 *mm. in length, and the diameter of their basal disc is about the same. The posterior half of the rostellum varies in appearance according to the state of contraction, and sometimes looks almost like a thin stalk on the thickened club-shaped anterior end. The first forty joints are of insignificant length and breadth. They occupy the foremost* 6 *to* 8 *mm. of the worm. But beyond that point the joints lengthen so much that they ultimately become four or five times as long as they are broad. In the meantime the breadth has also considerably increased* (*to* 2 *mm.*). *As their size increases, the joints are gradually more distinctly marked off from each other. The lines of connection are constricted, and the corners rounded off, so that the posterior half of the worm assumes a more and more decidedly moniliform appearance. The ripe proglottides are of a red colour* (*on account of the egg-masses shining through*), *and may be easily detached from the chain. Their number varies, according to circumstances, from ten to twenty-five, or even more. The male organs attain maturity at about the forty-sixth joint. By the sixtieth joint, the embryonic development is completed; and at the seventy-fifth the first distinct egg-masses may be seen* (0·07 *to* 0·2 *mm. in diameter*). *The latter have a roundish discoidal form, and contain, according to their size, a variable number of eggs, on an average two to three dozen. They are formed of a sharply defined firm cement of a brownish colour, and the number in each joint amounts to perhaps from* 350 *to* 400. *The isolated eggs measure* 0·05 *mm., and the embryo* (*with hooks of* 0·015 *mm.*) 0·033 *mm.*

FIG. 347.—*Tænia cucumerina* (nat. size).

The species which we have thus shortly described is by far the most frequent tape-worm in dogs and cats, or at least in those which are reared indoors. It generally lives socially, several hundred specimens being sometimes found side by side, and in some cases as many as 2000 (Krabbe). If cystic tape-worms be also present, they are always situated farther forwards in the intestine. Hence the worm

is usually found in the hinder part of the small intestine. Since it possesses a great elasticity, and can be drawn out almost like a thread to three or four times its usual length, the end of the chain is often found in the neighbourhood of the large intestine, in the interior of which the free proglottides, which are readily recognisable from their red colour and elliptical form, are usually accumulated in great numbers.

Although this worm is quite as frequent in the cat as in the dog, Linné has applied to it the name *Tænia canina*, which has since been changed more than once (by Pallas into *T. moniliformis*, and by Göze into *T. elliptica*). Rudolphi and his followers, indeed, believed that the worms found in the dog and in the cat should be distinguished as two distinct species[1] (*T. cucumerina* and *T. elliptica*), and at the time of the first edition of this work I was of the same opinion. But as the result of renewed and careful investigation, I am now obliged to agree with Göze, that it is impossible to discover any radical differences between them.[2]

If now it be asked on what grounds this *T. elliptica* is included among human Helminths, we may answer, in the following way:—

Linné, who first recognised *T. canina* as a specific form, and rightly regarded the bilateral position of the sexual opening as its most important character, also maintained that it was occasionally found in man.[3] He even asserted that such cases were known to him. But this assertion was gradually forgotten. Pallas contradicted it, while Göze, Bloch, and Rudolphi did not deem it worthy of mention. But, in spite of this, the worm deserves the place assigned to it by Linné,[4] although it occurs in man only occasionally and exceptionally, and usually only during childhood.

In the Museum of Comparative Anatomy in Halle, there is, among other Helminths, a preparation which, according to the label written by H. Meckel, contains a convoluted *T. canina*, Linn., which was voided by a boy called Krebs during his stay in the surgical wards of Blasius. Through the kindness of Professor Welcker, I have

[1] *Tænia elliptica* was also erroneously described as destitute of hooks.

[2] The fact that in the dog *Tænia cucumerina* often attains a larger size can hardly be considered as a specific difference, since the same is true of *Ascaris lumbricoides* and of *A. mystax*, when they occur in different hosts. Even the statement of Krabbe ("Rech. helminthol.," p. 40), that in Iceland the cat is exempt from this *Tænia*, while dogs frequently suffer from it, does not seem to me to decide the matter.

[3] "Amœnit. acad.," ii., p. 81.

[4] I now perceive that my statements in the first edition of this work (p. 402) regarding a *Tænia cucumerina*, which Eschricht had received as voided by a Moorish slave in St. Thomas, are based upon an error, since the parasite was not *T. cucumerina* but *T. cucurbitina* (= *T. solium*, Auct.) (See *Nova Acta Acad. Cæs. Leop.-Carol.*, Suppl. ii., t. xix., p. 139.

had an opportunity of examining these specimens, and have convinced myself that they belong to *T. cucumerina.* There are, perhaps, forty to fifty pieces, usually between 100 and 130 mm. in length, and the majority of them still without egg-masses. Unfortunately, I found it impossible to learn anything further regarding the boy Krebs, so that I am unable to decide whether his illness had any connection with the parasite. The supposition of an accidental mistake, or designed deception, is rendered highly improbable from the circumstances under which the patient lived.

This case in Halle is, however, not the only one which I can adduce. I owe a second to a communication from Dr. Weinland of Frankfort, whose name I have already so often had occasion to mention with gratitude. The case in question is that of a child thirteen months old, who from time to time voided single proglottides of small size and reddish colour, which were recognised by the attending physician, Dr. Salzmann, and by Weinland as proglottides of *Tænia cucumerina.*[1] Through Dr. A. Schmidt of Frankfort I soon afterwards became acquainted with a third case, and that, too, of a child, only, however, thirteen weeks old. The mother observed a portion, about six inches in length, protruding from the anus, tore it off, and brought it to Dr. Küster of Cronenberg, through whom it fell into the hands of Schmidt. The head was wanting, but the nature of the joints left no doubt regarding the nature of the worm.

Since the foregoing communications were published in the first edition of this work, our experience of the occurrence of *Tænia cucumerina* in children has increased so much, that the cases in question can no longer be regarded as specially rare. According to Krabbe, the worm occurs in man in Denmark, and according to Cobbold, in England, while no fewer than six cases have been brought under my own notice by different physicians.[2] It was always children between nine months and three years old who were infected with this tape-worm. The joints generally issued singly, sometimes spon-

[1] Salzmann has in the meantime himself described this case (*Wurtemb. naturw. Jahreshefte*, p. 102, 1861; *Froriep's Neue Notizen*, iii., 9, 1861; *Deutsche Klinik*, p. 32, 1861).

[2] I have not included among these the "*proglottides neonati*," mentioned in the first edition of this work, which were observed by Krämer (*Illustrirt. med. Zeitung*, Bd. iii., p. 295), who first described them as having a strong resemblance to *Tænia cucumerina.* Yet I have convinced myself, by the investigation of the original specimens preserved in the Pathological and Anatomical Collection at Göttingen, that they belong to this worm. The statement that "the latter, to the amount of about a teaspoonful, were voided by a newly born child about twelve hours after birth, and before it had received milk," is extremely incredible, and irreconcileable with our present knowledge of the life-history of *T. cucumerina.* It is much more probable that it was voided by a dog or a cat than from the child in question, which is described as perfectly healthy, and which never voided any more proglottides.

taneously (on one occasion through the nose), and sometimes with the stools, and continued moving for a time after their expulsion. According to the communications made to me, they had a length of 5 to 8 mm., and a breadth of 1·5 to 2 mm., exhibited the well-known red colour, and, if investigated in a fresh condition, contained the already described clusters of eggs. Schoch-Bolley of Zurich, who in one case succeeded in expelling entire worms by means of Kamala, while in all the other cases only portions were obtained, estimates the length of the worm at nearly a foot. As but two worms were voided in this case, it appears that *T. cucumerina* does not occur usually in such large numbers in man as in dogs and cats, and that in most cases only a few are found living together.

So far as I know, no symptoms of disease were observed in any of these cases. If a larger number of worms were present, it might perhaps be otherwise. At least it has been observed that under such circumstances dogs sometimes exhibit cramp and other symptoms of nervous or gastric disease. I have already (p. 143, note) quoted a case of this kind from Göze's famous "Naturgeschichte." A second one is cited in another part of this work from the observations of Wagler,[1] which, however, only differs from the former in the increased gastric disturbances.

Now, however, we are not only acquainted with the fact that *T. cucumerina* is by no means very rare in man during childhood, but have also learned the way in which children are infected; in other words, an unexpected disclosure has been made regarding the life-history of the worm.[2]

This discovery was made in the summer of 1868 by one of my Russian students, now Professor Melnikoff, while busied in my laboratory with investigations regarding the embryology of the louse. He was examining for the purpose the dog-louse (*Trichodectes canis*), and one day discovered in the body-cavity of this parasite (which, instead of the piercing and sucking mouth of *Pediculus*, is well known to possess a masticatory apparatus, and to gnaw the epidermis of its host), some small white bodies which he did not know how to interpret. After close investigation, I recognised them as the cysticercoid forms of *Tænia cucumerina*. The rostellum and the formation of the hooks removed all doubt as to the correctness of the diagnosis. Strange to say, the Cysticercoid was

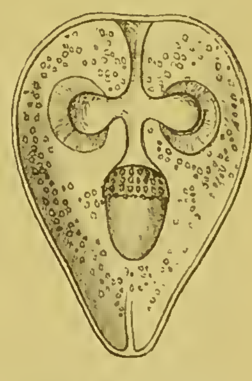


FIG. 348.—Cysticercoid of *Tænia cucumerina*. (× 60.)

[1] *Loc. cit.*, p. 324. [2] *Archiv f. Naturgesch.*, Jahrg., xxxv., Bd. i., p. 62, 1869.

without a proper caudal bladder. It is true that the entire attaching apparatus, including both suckers and rostellum, was retracted, but the envelope of the latter did not differ either morphologically or histologically from the rest of the body. The Cysticercoid appeared exactly like an *Echinococcus*-head with a retracted apex.

The intermediate host of *Tænia cucumerina* having been discovered,[1] it occurred to us that it might be possible to rear its Cysticercoids. A pulp, made of the ripe joints of the *Tænia*, was by my advice applied to a portion of skin upon which the *Trichodectes* were plentiful, and afterwards the first stages of the worm were sought for in these insects. These we succeeded in finding on several occasions, and for the first time seven days after the commencement of the experiment. They were in the form of club-shaped, six-hooked embryos, which had attained a length of 0·2 mm.—double their former size,—and lay free in the body-cavity. Regarding their origin, there could be no doubt from the six hooks still situated at the thinner end.

A comparison with the above-described Cysticercoids seems to suggest that the distended end of the body in this case becomes provided with hooks, and is then retracted into the dependent thinner part, but without the latter being formed into a special bladder-body, or producing the tape-worm head by endogenous budding. I may refer in this connection to the description which I have already given of the mode of development of the *Tæniæ* (p. 364).

These results reveal to us clearly and explicitly the life-history of *Tænia cucumerina*. The egg-capsules, which have probably been long preserved from desiccation, and have retained their power of development, make their way sooner or later (sometimes still enveloped by the proglottides, and at other times alone) from the excreta to the hairy skin of the dog, and thence to the *Trichodectes* living upon it, in the interior of which the eggs change into Cysticercoids. It is easy to see that dogs, which, like other animals, often lick themselves, and also directly prey upon their vermin with their lips and teeth, often find opportunities of devouring the hosts of these bladder-worms, and of course the more frequently the more that their condition and mode of life facilitates the transmission of the eggs, and the increase of the ectoparasites. Uncleanly kept house-dogs thus exhibit a peculiarly favourable combination of the conditions necessary for the development of *Tænia cucumerina*.

The infection of man takes place, as might be supposed, either through the tongue of the dog, which returns caresses by licking, or

[1] This demonstration, of course, showed that the former conjectures regarding the intermediate host of *Tænia cucumerina* (see first German edition, Bd. i., p. 404) were illusory. Even then, however, it seemed very likely that the latter would be an insect.

through the hands, which touch and stroke this animal. Thus in both cases the transmission takes place indirectly, and this explains why the tape-worm occurs in man only in small numbers, or even singly. In all cases the hosts have in some way or other come into close contact with the dog. Nor does it surprise us to learn that these hosts are most frequently children, since they generally treat dogs with the most unrestrained familiarity.

Hering, however, cannot reconcile himself to the significance which the change of hosts possesses in the life-history and circulation of the parasites, and is, moreover, of the opinion that the Cysticercoid state is by no means necessary to the development of *Tænia eucumerina* (nor, indeed, to any of the other tape-worms), and that the worm may be developed in the subsequent host, directly from the six-hooked embryo. To test the accuracy of this supposition, he fed fourteen dogs with the ripe terminal joints of *T. cucumerina*,[1] and afterwards found the tape-worm in twelve; but the various results agree so little with the stages of the experiment, and otherwise contradict each other so much, that the only thing that can be concluded from them is the great frequency of the parasite, and especially in young dogs, such as Hering used (Krabbe found *T. cucumerina* in 87 out of 185 cases in Copenhagen, or nearly half of the dogs which he examined in search of Helminths). But even if these feeding experiments are not conclusive, they are by no means without interest, since they show that the transformation of the Cysticercoid into the adult tape-worm only occupies a short time. For example, a dog only thirty-one days old was found to contain a *T. cucumerina* 15 inches long, and with perfectly ripe proglottides. Another dog ten days old contained a tape-worm 10 lines in length, with distinctly defined and already oval joints. The supposition that the dog is infected more easily by sucking its mother than by licking seems hardly probable from these cases, for then the date of the infection must coincide with the first day of life. We can therefore hardly be wrong in supposing that for its development from the Cysticercoid to the ripe proglottides, *T. cucumerina* requires about two to two and a half weeks.

In conclusion, a few remarks on the structure of the sexual organs may be added. It has already been mentioned in regard to these tape-worms that the genital pore, or rather the outlet of the sexual organs (since the male and female ducts open near each other without any special sexual cloaca) is double. One part lies on the right, and the other on the left lateral margin, both being about the middle, or but little behind it, as, indeed, may be observed with the naked eye,

[1] "Beiträge zur Entwickelungsgesch. der Eingeweidewürmer," *Würtemb. naturwiss. Jahreshefte*, p. 356, 1873.

even in the small joints, if they be compressed between two glass plates. In the ripe joint this double outlet is connected with a coiled vas deferens, and with a vagina. Before reaching the middle line, the latter comes downwards, and becomes united with two wing-like ovaries, and with a single yolk-gland.

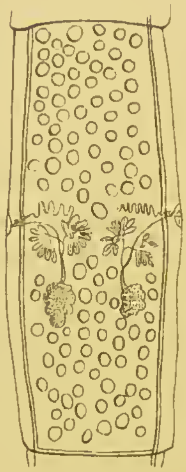


FIG. 349.—Proglottides of *Tænia cucumerina* in a sexually mature state. (× 20).

The former always consist of groups of branched tubules, while the yolk-gland exhibits a simple lobed structure. Between the two[1] lies a bladder-like receptaculum seminis, and farther down, where the sheath is connected with the yolk-gland, there is a shell-gland, which, as usual, is composed of a group of simple stalked cells.

Occasionally one finds joints with four genital openings and efferent canals. These are situated in pairs opposite to each other, and are separated by a wider space, so that in spite of their but slight increase in size, it seems most natural to regard them as double joints, which, as before, in the case of *Tænia saginata* (p. 450), may be ascribed to a suppression of the line of demarcation. On the other hand, one sometimes finds only a one-sided development of the sexual organs.[2]

The first rudiments of the genital organs are observed about the twentieth joint, in the form of a parenchymatous streak, which runs transversely through the whole breadth of the body. The organs first developed belong as usual to the male apparatus, which, in addition to the cirrhus and cirrhus-pouch, consists of the much-coiled vas deferens above mentioned, and of about 180 round testes, which are distributed over the whole joint.

The uterus into which the eggs are transferred from the shell-gland has at the time of sexual maturity the form of a network, whose cords run between the testicular vesicles, and are continued laterally into a number of cæcal tubes, which in many places protrude beyond the longitudinal canals. As the eggs gradually accumulate in the interior of the uterus, and as their size is gradually increased by the development of the embryos, both these tubes and the nodes of

[1] On this subject see Steudener's paper, "Untersuchungen über den feinern Bau der Cestoden" (*Abhandl. der naturf. Gesellsch. Halle*, vol. xiii., 1877), which in many particulars supplements my former communications.

[2] Salzmann has noted other abnormalities of this tape-worm. The male and female openings are, he says, sometimes widely separated from each other, and the male opening is occasionally wanting. Embryos with a larger number of hooks, such as those observed by Salzmann, have also been found by Ramsay-Wright and myself, p. 330.

the network are enlarged into roundish pouches. With increasing size, these become more and more sharply marked off from each other, and are distributed over the whole joint in place of the testes, which have in the meantime gradually atrophied. When the embryos are mature, the contents of these pouches are always enclosed in a common cementing substance, which is perhaps formed from the original contents of the uterine branches, and, on becoming firm, assumes a reddish-brown colour. The number of eggs adhering together is determined by the size of the pouches. I found some clusters with only eight or ten eggs (0·07 mm.), and others with seventy, or even more (0·25 mm.). The flat form of the masses is explained by the fact that the pouches are very closely packed, so that by mutual pressure they become flattened out, usually in the direction of the transverse diameter of the joint.

During the maturing of these egg-masses, not only the reproductive organs but the layers of substance lying between the pouches gradually disappear, as indeed Mehlis has remarked. In consequence of this the pouches coalesce, at first in the centre, so that the joint gradually becomes an almost saccular receptacle, in the interior of which the eggs remain until a rupture takes place and they are set free.

The calcareous corpuscles of *Tænia cucumerina* are somewhat numerous, although not so abundant as in the cystic tape-worms.

Family II.—Bothriocephalidæ.

The head is egg-shaped and flattened, sometimes in the same direction as the body, and then but slightly marked off from the latter; at other times in the opposite direction; with two longitudinal, more or less deep

Fig. 350.

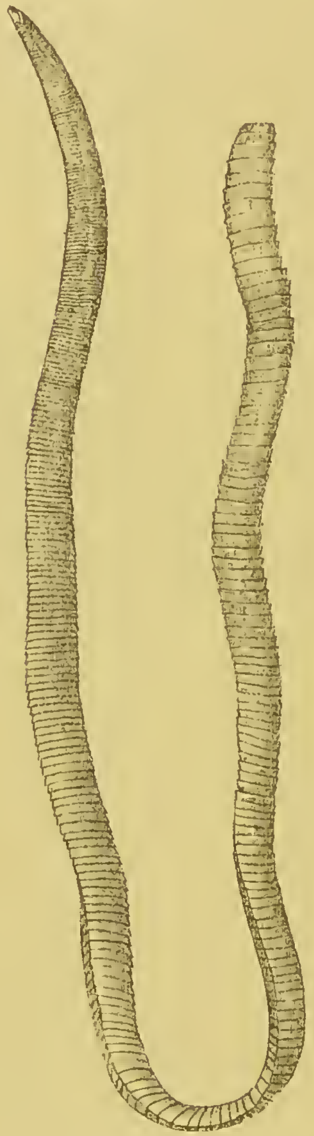


Fig 351.

Fig. 352.

Fig. 350.—*Bothriocephalus cordatus* of man (nat. size.)
Fig. 351.—Free swimming embryo of *Bothriocephalus latus.* (× 500.)
Fig. 352.—Larva of a *Bothriocephalus* from the skink. (× 20.)

suctorial grooves, which lie opposite to each other on the flat side of the chain, but are devoid of any special musculature. Similarly, the hooks,

if present at all (Triænophorus), *are without a rostellum. The segmentation is indistinct, and sometimes altogether absent, in which case the body has a very simple structure. The joints are always broader than long, and in their mature state so firmly united, that they are not detached singly, but in numbers. The uterus is a simple, more or less winding canal, with a ventrally situated opening, through which the eggs issue after the completion of the embryonic development. The reproductive organs persist throughout life, and constantly emit new products. The yolk-glands, which are of considerable size, are symmetrically divided between the two sides, and often distributed over the whole cuticular layer. The cirrhus and vagina generally open externally, not far from the uterus, and more rarely* (*as in* Tænia) *on the border. The eggs contain a considerable quantity of yolk, and possess from the first a firm shell, with an operculum at one end, so that the embryo can readily find an exit. The embryo is usually covered with a distinct ciliated mantle, by means of which it can swim about for some time.*

Except in the case of Archigetes, *the development of the larva takes place in an intermediate host, but in a somewhat direct way, for the embryo merely elongates, and forms the subsequent suctorial grooves. Sometimes it grows into a jointed tape-worm, even in its intermediate host; but as a rule this takes place only later, after the parasite has migrated from its original abode into the intestine of the definitive host. A true bladder-worm stage seems always wanting, but in some cases there is an appendage on the posterior border of the larval body, which in genetic significance corresponds to the caudal bladder of the* Cysticerci.

If we are right in ascribing the highest place among the Cestodes to the Tæniadæ, and especially to the cystic tape-worms, the family Bothriocephalidæ (in the sense here defined) must be regarded, on the contrary, as the lowest group. This is evident, however, not so much from the anatomical structure of the several organs, as from the fact that the individualisation of the different parts composing the body is upon the whole much less pronounced than in the other tape-worms, and in many cases is even completely wanting. The head, which is elsewhere a structure of great independence and characteristic structure, is small and simple, and often hardly other than the anterior end of the body provided with the attaching apparatus. Similarly, the segments are usually imperfectly separated, and sometimes not marked off in any way from each other, so that the segmentation is only shown by the regularly recurring sexual organs (*Ligula*, *Triænophorus*). But when, as in some cases (*Caryophyllæus*, *Archigetes*), the number of these structures decreases to one, the appearance presented is entirely different. In place of the polyzootic tape-worm there is a simple

animal, in which the various organs and functions, formerly distributed over different individuals, are united in one (p. 386).

The slighter individualisation of the different parts of the body also finds expression in the processes of development. Instead of the former features of an alternation of generations, we find in the Bothriocephalidæ modifications, which rather suggest a simple metamorphosis. The primary stages of development disappear, and there is a corresponding diminution in the difference between the larva and the adult worm. The larval form becomes like the sexually mature animal, and sometimes to such a degree, that they can only be distinguished by the imperfect development of the sexual organs in the former. This is perhaps most striking in the Ligulidæ (*Schistocephalus, Ligula*), which in their intermediate hosts, the stickle-backs and bleak (*Leuciscus*), not only grow to their full size, but form their sexual organs, which develop so far that, after the transference into the intestine of their definitive host (a piscivorous bird), maturity is attained in an exceedingly short time (p. 379). In *Archigetes* the whole development takes place in the intermediate host. So far as we know (p. 378), it is the only tape-worm that undergoes no change of host, and that never loses the characteristics of its larval life.

Fig. 353.—*Archigetes Sieboldi.* (× 60.)

Fig. 354.—Larva of *Bothriocephalus latus.* (× 55.)

These are, however, mere exceptions. Usually, the larval forms of the Bothriocephalidæ are easily distinguished from the adult worms, not only because they are destitute of reproductive organs, but also because they are unsegmented (Fig. 354). They possess, as a rule, a longer or shorter, ribbon-like body, whose anterior end bears the suctorial grooves, and is thereby recognised as the head.

It is doubtful whether the ribbon-shaped posterior part of the body is always cast off, as in the *Cysticerci*, on the transition to the final state; and that the more, since the head of these worms hardly ever attains its full development and size during the larval life, but only after the transference to the alimentary canal of the definitive host.

The Suctorial Grooves in the larval forms are often shallow and indistinctly limited in comparison with the subsequent general pro-

minence which they afterwards attain. They exhibit also in the adult many differences, both in form and size, which are for the most part correlated with the structure of the head. When the latter is broad the suctorial grooves are usually oval or patelliform, but when the head is transversely compressed they appear as longitudinal clefts, limited by projecting lips, and extending more or less deeply inwards; often also widened internally, or even continued for some distance backwards into a cæcum.

During life the suctorial grooves are in constant movement,—sometimes drawn out, sometimes contracted, according to the changes of form exhibited by the head. The lips, too, open or close according to circumstances. Here and there the head may be seen retracted in the body-mass.

The Musculature of the head and of the suckers is, however, much simpler than that of the Tæniadæ,—so simple, in fact, that it can without difficulty be derived from that of the body generally.[1] The greater simplicity lies especially in this, that the cup-shaped musculature, which is so conspicuously characteristic of the suckers of the Tæniadæ (and also of the *Tetrarhynchi*, &c.), is not developed in the forms now under discussion. The muscles which here supply the suckers are integral parts of the general musculature of the body, directly continuous with them, and only differing in their adaptation to specific functions of the attaching apparatus.

The general musculature differs further from its typical disposition of the Tæniadæ in this, that the longitudinal fibres extend in a continuous strand through the whole chain, and do not of course exhibit those metameric interruptions which we have described (p. 293) in those *Tæniæ* which liberate individual proglottides.

The first modification which these muscles exhibit within the head consists in the loss of that distinction between the cortical and median layers which is so characteristic in the other parts of the body, and especially in the sexually mature joints. Longitudinal and transverse fibres lose their former disposition, and are distributed, becoming at the same time thinner, with some uniformity over the whole internal parenchyma of the head. Even the cellular layer of the subcuticula is abundantly penetrated with fine fibres. This is especially true of the subcuticula of the suckers, which not only exhibits numerous sagittal fibres, but is also penetrated by transverse strands. These continue out to the structureless external cuticle, and pursue a course corre-

[1] See in this connection Sograff's description of the structure of the head of the Bothriocephalidæ in the *Trans. Friends of nat. hist.*, *Moscow*, vol. xxiii., part 2, p. 21 (Russian), which is, however, incomplete after my investigations which relate especially to *B. latus*.

sponding to the form of the head. They are not, however, stretched, as in the jointed body, but are disposed in curves corresponding to the concavity of the suckers. Towards the sides the fibres separate in a fan-like manner, until they severally reach the external surface of the head, and are there inserted. Their function is probably to bring together the lateral portions of the head, which extend as sort of lips beside the suctorial grooves, and thus to narrow the grooves and assist fixation.

The effect of these muscles is increased by fibres, which are disposed at right angles to the internal cavity of the grooves, and which probably play the same *rôle* as the radial muscles in the suckers of Tæniadæ. In the median layer of the head, between the two grooves, these fibres are stretched, as ordinary sagittal muscles, between the dorsal and ventral surfaces, while they extend transversely in more or less diagonal course, through the lip-like projecting lateral borders.

The longitudinal fibres exhibit a disposition which, like that of the transverse strands, is conditioned by the form of the head. They are not limited to the middle portion alone, but traverse, in considerable numbers and in closely packed groups, the lateral portions, which project dorsally and ventrally, so that they form in cross section an almost H-shaped figure. Their contraction causes a shortening of the head, and especially of the lips, in consequence of which the latter are slackened and lose their grip. The longitudinal fibres are therefore to be regarded as the antagonists of the other head muscles described above. They are aided to some extent by fibres which pertain to the convex external surface of the head, and pass from one region to another like tendons, with spans of varied length. Although but weakly developed and few in number, they are probably sufficient to approximate the margins of the external surface, and thus to separate the lips of the suckers and widen the grooves.

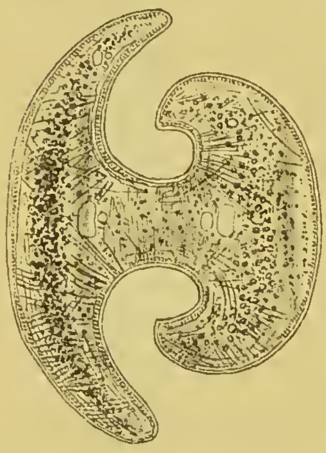


FIG. 355.—Transverse section through the head of a young *Bothriocephalus latus*. (× 55.)

The Cutaneous Glands.—In well-stained heads of *Bothriocephalus latus* (and it is only in such that the fibrous strands here described can be clearly followed) one can detect between the spindle-shaped cells of the subcuticular layer, both in the suctorial grooves and elsewhere, a number of intensely stained bodies of bottle-like shape (0·017 mm. long by 0·008-0·01 mm. broad), which have their necks turned outwards, and which sometimes allow their contents to pass out in the

form of a small drop.[1] One is at the first glance perhaps inclined to regard these structures as forming an absorption-apparatus, but the impossibility of tracing their contents into the body-parenchyma leads to the supposition that they are structures of a glandular nature, such as occur with more or less frequency in other flat-worms. Their absenee in the segmented body, and the fact that they have not been as yet detected among other Cestodes, can hardly be urged as an argument against the above interpretation. They serve, perhaps, for the secretion of a mucus or even viscid substance, which facilitates the attachment of the worm.

The Two Nerve Cords are seen through the head with no less distinctness than the muscle-fibres. They are found at that region where the middle portion passes out into the side, in a position which corresponds topographically to the lateral margins of the jointed body, and whieh is especially marked in the head, since the sagittal and diagonal muscle-fibres which are attached to the internal surface of the grooves leave a free triangular space at this point (Fig. 355). The nerve strands are seen as two roundish or kidney-shaped spots of granular appearance, which gradually approach one another towards the anterior end of the head, and are finally united in a loop by a transverse connective.

Internally, the nerve strands are aceompanied by a longitudinal vessel, the eross section of which can be traced throughout the head. even far forward. Besides this, there may be observed in *Bothriocephalus latus* a number of fine vessels whieh extend below the subcuticular layer of cells, and are sometimes united to each other by a lateral braneh.

The Excretory Apparatus of the Bothriocephalidæ has, as has been already noted (p. 301) by no means the well-known rope-ladder disposition exhibited by the Tæniadæ. Not only do the lateral stems (exeept in the head) exhibit a retieulated disposition, the result of repeated division and anastomosis, but these deeper canals are assoeiated with a superfieial system of fine vessels, which also form a connected network, and are distributed over the whole body. The opinion was formerly held that this fine network represented the proper secretory surface of the apparatus, and to this I myself formerly inclined, but the researches of Pinter[2] and Fraipont[3] have

[1] I describe these structures from a preparation given to me by Braun, which was made from the head of a *Bothriocephalus* four days old, from the alimentary canal of a cat. Braun also found these bodies "of doubtful import" in the *B. latus* of the dog ("Zur Entwicklungsgesch. d. breiten Bandwurmes," Tab. ii., Fig. 16, p. 55).

[2] "Unters. üb. d. Bau d. Bandwurmkörpers," *Arb. zool. Inst. Wien*, Bd. iv., 1880.

[3] "Rech. s. l'appareil excréteur des Trématodes et des Cestodes," *Archiv. d. Biol.*, t. i. and ii., 1880 and 1881.

lately led to another view of the nature of these structures. We now know that in all tapeworms, and not only in the Bothriocephalidæ, numerous extremely fine tubules, hitherto unobserved, are attached to the greater vessels, originating separately from the latter, extending undivided close under the surface of the body, and ending, after a longer or shorter course, in a small goblet-shaped enlargement (0·008 – 0·01 mm. long, by 0·004 mm. broad). The opening serves for the reception of large cell, rich in protoptasm, and on this is seated a cilium which hangs freely into the funnel. These cells are probably the proper secretory organs. They represent, according to Pintner, a system of unicellular glands, whose secretion flows through a more or less long, capillary, efferent duct to the tubular apparatus.

The ciliated lappets, which have been repeatedly described by earlier observers (p. 302), are all to be referred to these ciliated funnels. In the vessels themselves structures of this kind are never present. The earlier opinion to the contrary originated in an illusion, occasioned by the presence of ciliated funnels above or below the vessels.

A terminal vesicle is present in the Bothriocephalidæ only in the young stage, before any segments have been separated off. Afterwards, the longitudinal vessels seem to open independently, as is (according to Pintner) the rule also in Tæniadæ. There are, however, numerous observations as to the presence of special marginal pores, by which the longitudinal ducts open to the exterior through short transverse vessels. Pintner describes such openings in *Caryophyllæus* and *Triænophorus*, and Fraipont in various *Scoleces* and in *Bothriocephalus punctatus*. In the last, these "Foramina secundaria" exhibit a certain degree of regularity, being usually situated in twos or at most fours, at the base of the several segments. With this agrees Riehm's observation, according to which, in *Schistocephalus* (as I have been able also to convince myself), an excretory aperture lies on the right and on the left side of every segment.

The Generative Organs exhibit peculiarities to which we have already called attention (pp. 308, 317), distinguishing them clearly from the Tæniadæ. These peculiarities may be, for the most part, traced to the fact that the uterus, instead of being closed, as in the Tæniadæ, opens externally by a special aperture. The presence of this uterine aperture not only permits of an early liberation of the ova, but also of a continued functional activity, which of course further presupposes that the generative organs (and especially the yolk-gland) possess a very considerable development, and persist throughout their life in complete integrity, while in the Tæniadæ they degenerate after the passage of the ova into the uterus.

With the persistence of the generative glands is further associated the necessity of enveloping the ova, which are liberated very early (even before the development of the embryo), in a resistant shell (p. 321). The free mobility which is exhibited by the great majority of embryos of *Bothriocephalus* may also be so far associated with the early liberation of the ova, since it replaces the movement of the proglottides, increasing the chances of the developing brood reaching its destination.

FIG. 356.— *Archigetes Sieboldi.* (× 60.)

The separated segments do not for long retain the free and independent mobility which characterises the proglottides, especially of the large-jointed Tæniadæ. This is evidently the necessary consequence of their mode of separation which does not take place in single segments, but in longer or shorter pieces, which remain united.[1]

The adult Bothriocephalidæ live either in cold-blooded or warm-blooded hosts, but only in carnivorous forms, and almost always in those which feed on water animals, and especially on fishes. Besides predacious fish, these parasites especially infest water birds and seals. I say especially, for there are also several land animals, mostly mammals, which under certain circumstances harbour Bothriocephalidæ. *Archigetes* is a unique and conspicuous exception, both in its occurrence and in its whole life-history, since it attains sexual maturity, as has been already more than once mentioned, in the intermediate host, and that a worm.

The Distribution of the sexually mature worms suggests an inference as to the occurrence of the young forms. The embryos attain development especially in fishes, and more frequently in those inhabiting rivers, than in marine forms. The other vertebrate groups are not, however, wholly spared; young Bothriocephalidæ have been found in frogs and reptiles, in birds and mammals (species of *Sparganum*, Dies., and *Ligula*, Dies.), and even in animals which are only temporarily associated with water. Even man is in this connection, as we shall see, no exception.

[1] According to the observations of Eschricht and others, there are, indeed, in fishes some *Bothriocephali*, which regularly throw off all their joints during summer, so that only the heads remain, again producing during winter new segments, all attaining sexual maturity. In such cases the liberation of ova is not continuous, but periodic. To these belong, apparently, those species especially which produce naked embryos, developing within the joints, from thin shelled ova, with but little included nutritive material (p. 327); species, therefore, which in their mode of reproduction present considerable resemblance to the Tæniadæ.

The larvæ are sometimes found, as in *Sparganum*, between the muscles, usually, however, encapsuled in the liver and other viscera,—in localities, therefore, which we have already noted as the favourite haunts of bladder-worms. In many cases at a certain stage they leave their original resting-place, and pass into the body-cavity. This is especially true of those species which attain a considerable size within the intermediate host, particularly of *Schistocephalus* and *Ligula*, as we have already noted (p. 676). The latter is found in the body-cavity of bleak, and sometimes a foot long and correspondingly broad, so that in a few days it may attain its complete development in the alimentary canal of a duck or goosander (*Mergus*). The unsegmented *Triænophorus*, with its two pairs of forked hooks, is also not unfrequently found of a finger's length within the body-cavity of the salmon or pike, within which, like the strap-worm (*Ligula*), it breaks through its cyst when the latter becomes too thin to envelope the growing worm any longer.

There are altogether but few genera included in the family Bothriocephalidæ, as above defined. Of these only one claims special attention here—*Bothriocephalus*, which, apart from the doubtful *B. cristatus*, Dav., includes two species parasitic in man—(1.) *B. latus*, the "Fascia" or "Tænia" of Plater and Andry (p. 410), whose true nature was first recognised by Bremser in 1812; and (2.) *B. cordatus*, first described by myself. To these must be added an unsegmented species, which, in spite of its considerable size, is shown by its structure and immaturity to be only a young form of a *Bothriocephalus*. This worm was sent to me long since from Japan by Dr. Scheube, and is identical with the Chinese form, since described by Cobbold as *Ligula Mansoni*.

Bothriocephalus, Rudolphi (*sensu stricto*).

Dibothrium, Diesing.

The head is without hooks, and is distinctly marked off from the long segmented body. Cirrhus and vagina usually open on the ventral surface of the joints before the uterus; rarely at the margin. The uterus, filled with ova, lies in the middle of the segments in the form of a coiled, often rosette-shaped canal. In the larval form the body is unsegmented, but more or less long, and ribbon-shaped.

The genus *Bothriocephalus* was first established by Rudolphi in his famous "Entozoorum historia naturalis" (1809). In its original connotation it included all jointed tape-worms, which are provided,

not with the suckers (oscula suctoria) characteristic of the genus *Tænia*, but with suctorial grooves (bothria). This included forms of very varied structure, with two or with four grooves, and with or without hooks on the head. These were afterwards classified, and that almost contemporaneously, by my uncle, Fr. S. Leuckart, in his well-known monograph of the genus *Bothriocephalus*,[1] and by Rudolphi himself (1819) in his "Entozoorum synopsis." The genus was, indeed, conserved in its whole extent, and indeed enlarged by my uncle to the extent of including the segmented *Tetrarhynchi*, previously separated by Rudolphi; but within the genus both Rudolphi and Leuckart distinguished, according to the structure and armature of the head, a number of smaller groups, which are still, for the most part, retained, except that they now represent genera or even families. The species which remain after the separation of the *Tetrarhynchi* are those which, in Rudolphi's system, formed the "Inermes (gymnobothrii) dibothrii" of the first group, which Diesing afterwards collected under the generic name *Dibothrium*. Including several doubtful forms, the latter enumerated in this genus thirty-two species, all of which, with the exception of one doubtful case, infest the alimentary canal of mammals, birds, or fishes. The suctorial grooves are said to be sometimes marginal, sometimes placed on the flat surface; but recent investigations seem to have made it questionable whether any forms with marginal grooves really exist. The description, formerly so generally accepted, has, in the case of *Bothriocephalus latus* at least, proved to be erroneous.

Bothriocephalus latus, Bremser.

Tænia lata, Linné, *incl.* T. vulgaris, Linné, *et* T. tenella, Pallas.

Bremser, "Lebende Würmer im lebenden Menschen," 1819, pp. 88-96.

Bötticher, "Studien über den Bau des Bothriocephalus latus," *Archiv f. pathol. Anat.*, Bd. xxx., pp. 97-148.

Short-jointed, broad and flat, of considerable length—up to 8 *to* 9 *m., but usually shorter. The number of segments amounts, in long specimens, to at least* 3000 *to* 3500. *With the exception of the last few, the joints rarely measure more than* 4 *to* 5 *mm.* (*usually* 3 *to* 3·5 *mm.*) *in length, while their breadth increases gradually to* 10 *or* 12 *mm. and more* (*occasionally to as much as* 20 *mm.*). *Posteriorly, the proportions are somewhat altered, inasmuch as the breadth of the segments decreases and the length increases, until the previous form is replaced by a square, or even slightly elongated rectangular form. The body is usually thin*

[1] "Zoologische Bruchstücke," i.: Helmstedt, 1819.

and flat, like a ribbon, especially towards the sides, while the median portion, which contains the uterus, projects as a sort of pad. The

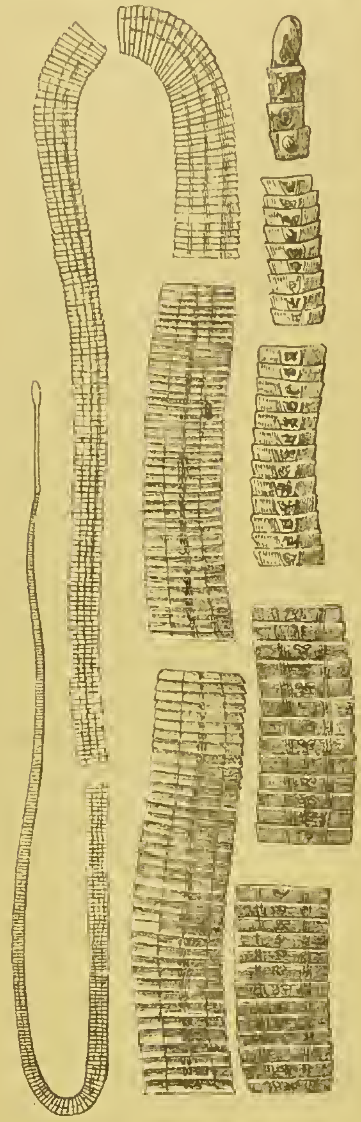


FIG. 357.—*Bothriocephalus latus* (nat. size).

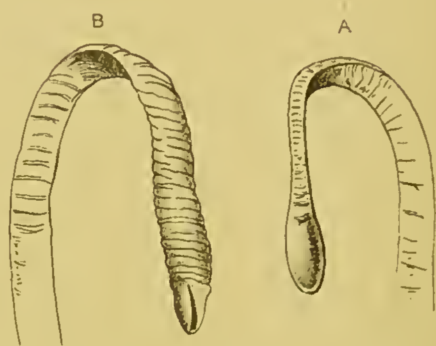


FIG. 358.—Head of *Bothriocephalus latus.* (× 8.) *A*, From the flat side ; *B*, From the margin.

anterior end of the body is sometimes much contracted, and is then relatively broad; sometimes, however, elongated and thin, or even drawn out into a thread-like neck, so that the head, measuring 2 *to* 5 *mm. in length and* 1 *mm. in breadth, is marked off as an elongated swelling. Viewed from the side, the head usually has, during quiescence, the form of a more or less elongated oval, with rounded, or occasionally with somewhat pointed, anterior end. A shallow furrow, which extends along the margin of the latter, is continued posteriorly directly into the suctorial groove, which can be traced to the hinder end of the head in the form of*

a deep longitudinal cleft between the usually curved or wavy lips. The proportion of the body occupied by the barren joints varies according to the form of the worm. When the anterior portion of the body is much thickened, one finds the first ripe ova 500 *to* 600 *mm. behind the head, in segments which are about* 5 *mm. broad and* 2 *mm. long, and which are preceded by at least* 600 *immature proglottides. The number of eggs is at first small, but it increases so greatly that the substance of the body is not unfrequently raised up into a sort of vesicle.* Pari passu *with this increase, the modification of the uterus progresses. It lies at first coiled up in the middle of the joint, extending from behind forwards; but afterwards, when a larger number of ova are collected, and when the uterus has in consequence increased in length beyond the limits of the joint, it is disposed in a loop-like fashion right and left. In this way there is formed in the middle of the mature joints that peculiar stellate or rosette-shaped figure, which has been compared to a flower (Linné) or heraldic lily (Pallas), and has been from of old regarded as the most striking characteristic of the species. The loops lie in close proximity to one another, projecting towards the sides like the leaves of a rosette ("horns"). There are generally four or five of these on each side, and more rarely six. They are approximated to various degrees, according to the state of contraction of the segments, but are always so grouped that the anterior include the generative apertures between them. These latter are surrounded by numerous papillæ. The cirrhus-pouch opens along with the closely adjacent vulva into a common transverse slit. The opening of the uterus lies a short distance behind. The yolk-sacs are embedded in the cortical layer of the lateral regions, both ventrally and dorsally, are seen as dark points through the otherwise almost transparent parenchyma, and give the sides of the body a yellowish grey appearance. The greatest development of the uterus, which corresponds with the greatest breadth of the worm, does not, however, coincide with the limits of the middle portion, but is found at a considerable distance further back. Stretches of joints of some length, and not individual proglottides, are separated off, and the line of division always passes through the anterior half of a joint. The muscular layers are, on the whole, but slightly developed, and calcareous corpuscles have only a scattered distribution throughout the body. The eggs have an oval form, and average in diameter* 0·05 *mm. and* 0·035 *mm. They are enveloped in a simple brown shell, provided with a lid with a distinctly defined margin.*

FIG. 359.—Eggs of *Bothriocephalus latus;* one of them after the liberation of the yolk contents. (× 300.)

The larval form lives encapsuled in the pike, in the burbot (Lota vulgaris), *and probably in other river fishes. It rests between the muscles,*

or in various viscera. It is of inconspicuous size (5 *to* 10 *mm.*), *and has a flat club-like shape. The head is furnished with two superficially situated suctorial grooves, and is usually retracted.*

Although this worm differs strikingly from the *Tæniæ* in the form of the head, in the structure of the uterus, and in many other details of organization, it was, till the seventeenth century, associated with the large-jointed human tape-worms, and especially with *T. saginata.* Its occurrence in the alimentary canal of man, and the general resemblance in form and size, counterbalanced a number of differences, which were neither understood nor adequately appreciated.

As we have already mentioned (p. 410), Felix Plater in Basel was the first to emphasise the differences between these two parasites, and to demonstrate the occurrence in man of two distinct species of tape-worm, which were for long distinguished as *Tænia prima* and *T. secunda Plateri.* Towards the end of the seventeenth century, the once renowned helminthologist of Paris, Andry, bestowed on the *T. prima* of Plater (*i.e.*, on our *Bothriocephalus*) the title "Tænia à épine" (*T. vertebrata*) on account of the external protruding middle region, and almost vertebra-like disposition of the uteri. Fifty years later Bonnet emphasised the "stigmata umbilicialia" of this worm in contrast to the "stigmata lateralia" of what we now call *Tæniæ*, and in the designation "Tænia à articulations courtes" directed attention to the physiognomic difference, at once obvious in contrast to the large-jointed tape-worms, "Tænia à anneaux longs."

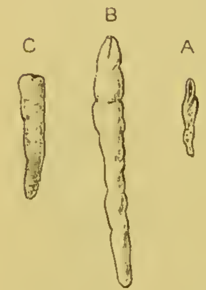


FIG. 360.—Larvæ of *Bothriocephalus latus* from the pike. *C* with retracted head. (*A* nat. size, *B* and *C* × 2).

Important as these results were in the progress of our knowledge, it is to be deplored that Bonnet, in consequence of a confusion, equipped his worm with the head of a *Tænia saginata.*[1] Although the renowned naturalist of Geneva himself recognised his mistake thirty-four years later, and corrected it by a description of the head of a true *Bothriocephalus* (p. 413), he had unfortunately done much in the meantime to establish the opinion that two kinds of short-jointed tape-worms occurred as parasites in man, viz., the *T. vulgaris*, L. (= *T. grisea vel membranacea*, Pallas) and the *T. lata*, L., which latter was supposed to unite the structure of a *Bothriocephalus* with a hookless Tænioid head. Pallas thought he was even warranted in establishing, under the title *T. tenella*, a third species, with joints like those of *Bothriocephalus.*

[1] *Mém. math. et phys. acad. roy., Paris,* t. i., p. 473, 1850.

It was only after Bremser had, in his beautiful researches, confirmed Bonnet's correction as to the structure of the head in the short-jointed tape-worm, and had, for the first time, given a thorough and faithful description and figure of the worm, that the errors of earlier naturalists were explained. Since then it has been seen that the worm under discussion is no *Tænia*, as Rudolphi still maintained, but belongs to the genus *Bothriocephalus*, thus representing a group of tape-worms otherwise not widely distributed among Mammalia. It is only lately that we have become acquainted with forms infesting the seal, polar bear, cat and dog, in regions where fish are plentiful, which closely approach in structure and size the *Bothriocephalus* of man, much more closely than the species occurring in fish, which are mostly considerably smaller than *B. latus.*

But even Bremser allowed an erroneous description to persist, which was only corrected about two decades ago by the researches of Bötticher already referred to. The mistake related to the position of the head, the compression of which was, according to previous representations, parallel to that of the body, while it is in reality in a plane at right angles to the latter, so that the suckers belong to the flattened sides and not to the margins, as was supposed. It is not difficult, on examining well preserved specimens, to corroborate Bötticher's result.[1] On the first head of a *Bothriocephalus* which I saw, and before the appearance of Bötticher's memoir, I remarked the error of the old description, and corrected my former representation.

In the position of its suckers, this *Bothriocephalus* does not, therefore, differ from the other species of the genus. It is in correspondence with its occurrence and habitat that the suckers of the worm, which lies with its surface adjacent to the wall of the gut, should be turned towards the villi on which they are fastened.

The Anatomy of Bothriocephalus latus.

Eschricht, "Anatomisch-physiologische Untersuchungen über die Bothriocephalen," *Nova acta Acad. Cæs. Leop.-Carol.*, t. xix., Suppl. ii., pp. 1-152, 1841.

Leuckart, "Parasiten," first edition, Bd. i., pp. 423 *et seq.*, 1863.

Bötticher, "Studien über den Bau des Bothriocephalus latus," *Archiv f. pathol. Anat. u. Physiol.*, Bd. xxiii., p. 108, 1866.

Stieda, "Ein Beitrag zur Anatomie das Bothriocephalus latus," *Archiv f. Anat. u. Physiol.*, Jahrg. 1866, pp. 174-212 (Nachtrag, 1867, p. 61).

Sommer und Landois, "Ueber den Bau der geschlechtsreifen Glieder des Bothrioce-

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[1] Yet Küchenmeister, in 1879, describes the suckers of this *Bothriocephalus* (Parasiten, second edition, p. 243) as suctorial grooves flat, lateral, in the same direction with the margins of the body ("Foveæ marginales").

phalus latus," *Zeitschr. f. wiss. Zool.*, Bd. xxii., pp. 40-99, 1872 ; also as first part of "Beiträge zur Anatomie der Plattwürmer," Leipzig, 1872.

Moniez, "Mémoire sur les Cestodes," pp. 125-183, Paris, 1881 ; also in *Traveaux de l'Inst. de Lille*, t. iii., fasc. 2.

When, in the year 1860, I was working at the structure of this worm in preparing the first edition of this book, only the first of the above-named memoirs had been published, and although it still forms the basis of our knowledge of the anatomy of *Bothriocephalus*, it is markedly defective, in the absence of any discussion of the relations of this species to the other Cestodes. This defect tended to produce the impression that the peculiarities of *Bothriocephalus* were much more fundamental than is really the case. What Eschricht omitted, I have attempted to supply. Since then we have learnt that this worm is, in its general structure, at least in the general disposition of its organs and in the nature of its tissues, closely allied to the *Tæniæ*, although strikingly different from them in other respects, especially in the structure of its generative organs. In my description of the latter I unfortunately fell into a misconception in regard to the yolk-gland, which had been rightly interpreted by Eschricht and subsequently by v. Siebold, but which I mistakenly regarded as a deposit of excreted matter. To Stieda is due the credit of discovering this error, as also of elucidating our conception of the structure of the genital apparatus by his discovery of the vaginal sheath, which had been overlooked. What subsequent investigators have done has been essentially little more than an extension and correction in matters of detail. We shall find occasion to allude to these contributions in the description which follows.

As we have already noted, *Bothriocephalus* agrees in its general structure with the *Tæniæ*. In both can be seen (best in thin transverse sections) the same cuticle, with the subjacent, crossed fibrous layers, the same cortical and central layers, and the same disposition of the generative organs. The latter lie, as in *Tæniæ*, for the most part within the central layer, the male generative glands and the vas deferens turned to the dorsal surface, the uterus and ovary towards the ventral, where the generative openings are also situated. The only thing which seems unusual in *Bothriocephalus* is the presence of numerous large heaps of granules, lying in a layer between the subcuticular layer and the longitudinal cortical muscles, which they push out to a considerable extent, especially in the lateral regions of the segments. These are the structures which I formerly erroneously regarded as deposits of excreted substance, although they had been already shown by Eschricht to be connected with the female organs, and had been described as organs which, though not ovaries, played a

rôle in the equipment of the eggs, and were, in other words, as v. Siebold first precisely defined them, *yolk-glands.*

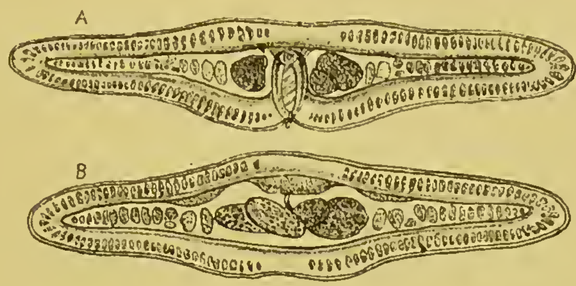

FIG. 361.—Transverse sections through the body of *Bothriocephalus latus.* *A*, At the level of the cirrhus-pouch ; *B*, In the posterior half, through the female generative organs. The testes, uterine horns, yolk-sacs, and nerve cords are also seen. (× 10.)

The Muscle Layers, like the reproductive organs, are disposed as in the *Tæniæ.* It is not of much importance that the longitudinal fibres of the cortex are more thickly packed towards the yolk-glands, and therefore towards the outside, than in the neighbourhood of the central layer, which in the *Tæniæ,* on the contrary, exhibits the greater number of fibres. Nor is it very remarkable that the musculature of this *Bothriocephalus* is inferior in strength and degree of development to that of the large-jointed tape-worms, and especially to that of *T. saginata.* There is further a difference between the two forms, in that the sagittal fibres of *Bothriocephalus,* instead of being uniformly distributed, are in the middle layer for the most part grouped in strands, forming a sort of framework in which the testicular vesicles and the uterine coils are embedded. In the younger joints this disposition is not yet perceptible; it only arises in consequence of the increase in the size of the generative organs, by which the adjacent fibres are pressed to the side.

The Connective Tissue consists of cells of unusual size, and more sharply defined than in the case of most Cestodes. This is in part due to the nature of the protoplasm, which is marked off as an almost gelatinous clear mass from the duller intermediate substance, and in part also to the development of a fibrillar network, which envelops the cells in its meshes. The vesicular tissue in the median region is most distinct and beautiful, especially in the neighbourhood of the cirrhus-pouch, where the cells not unfrequently grow to the size of 0·026 mm. and more. The fibrous network is here most strongly developed, and may be frequently observed to be of distinctly muscular character, since the fibrils are seen to come into connection with the processes and terminal branches of the true muscle-fibres.

Towards the sides the cells become smaller and less distinctly limited, sometimes so slightly that the ground substance presents in some parts the same appearance as in the *Tæniæ*. The layer of subcuticular spindle-cells is especially well-defined from the vesicular tissue.

The Calcareous Corpuscles (Kernkörnchen, Eschr.) of *Bothriocephalus*, as we have already noted, occur separately, and on the whole but sparsely.[1] They are at once most abundant and largest (up to 0·015 mm.) in the immature joints. They are especially met with between the longitudinal fibres of the cortex, but they are not wholly absent in the central layer. It appears, indeed, as if the individual specimens exhibited great variations in the number of calcareous corpuscles present. In the ripe old joints they seem not unfrequently altogether absent.

The Longitudinal Vessels and nerves, which have been already (p. 679) described within the head, may be traced in transverse sections nearly to the sexually mature joints. They differ only in so far as they increase with the growth of the body, though not in the same proportion. With this increase in thickness a larger space is left between them. They are not to be looked for, as in the *Tæniæ*, in the outer angles of the middle layer, but, as Eschricht observed, further inwards, near the middle of the two lateral regions (Fig. 361).

In the ripe segments the relations are changed, since the vessels, which elsewhere hardly ever measure more than 0·07 mm., and are also considerably less in width than the longitudinal vessels of the *Tæniæ*, gradually become narrower till at last they are no longer recognisable. They share the fate of the vessels which extend beneath the subcuticula, traces of which I was able to follow on my sections only as far as the neck. It cannot, however, be concluded that the vessels cease here, but only that in hardened specimens they are no longer to be detected, owing to their thinness, and the insufficient resistance of their walls. For the elucidation of the course of the vessels in *Bothriocephalus*, fresh specimens are necessary, and these are not always procurable. This being so, it is readily intelligible that the whole structure and disposition of the vascular system in this worm have not yet been elucidated. We do not know whether the longitudinal vessels, in their course backwards, remain undivided,

[1] Landois and Sommer, and Moniez are mistaken in asserting that, in the first edition of this work, I wholly denied the presence of calcareous corpuscles in *Bothriocephalus*. I have always spoken only of a relative absence, and on page 425 have, in noting their size, expressly stated that they agree in appearance and nature with those of the larger *Tæniæ*.

or, if connected, how this takes place. Only so much has been found out, that, besides the longitudinal vessels extending internally, a fine superficial vascular network is present here, as in other species. This has not only been established by the facts which we have already communicated, but has also been corroborated definitely and in detail by the results of Knoch[1] and Bötticher,[2] who have observed in the head of *Bothriocephalus* a close network of fine vessels, which becomes posteriorly coarser and more widely meshed, and finally (according to Bötticher) passes on each side into several wider longitudinal vessels, which are mutually connected by an irregular anastomosis. Moniez estimates the number of these superficial longitudinal vessels at about twenty. As to the connection with the more deeply situated longitudinal vessels, nothing is known, nor has any ciliation been yet observed in *Bothriocephalus latus*.[3]

The Nerve Cords, which can be traced along the whole length of the body, and which with increasing size of the joint become gradually thicker (from 0·25 mm. up to 0·1 mm.), change their position after the disappearance of the deeply seated longitudinal vessels, inasmuch as they are pressed not only farther inward in consequence of the stronger growth of the lateral borders, but also towards the ventral transverse muscles by the testicular sacs on the dorsal surface. They exhibit the same apparently spongy structure as the nerve tracts of the *Tæniæ,* and, like the latter, have been designated by Sommer "plasmatic" longitudinal vessels. Other observers have compared them to the longitudinal canals of the *Tæniæ,* except Eschricht, who thought he had discovered in them the limbs of a bifurcated divided alimentary canal. Cerebral ganglia, if present at all as distinct structures, are at any rate very small and insignificant, as the absence of specialised suckers would indeed lead us to suppose. It seems probable that the two lateral cords are united at the anterior end of the head by a simple transverse connective.

The peculiarities of *Bothriocephalus,* as above noted, may scarcely appear very striking or characteristic; but it is very different when we turn our attention to the next group of organs.

The Reproductive Organs.—In the nature and disposition of the genital apertures, in the structure of the uterus, in the arrangement

[1] "Naturgeschichte d. breiten Bandwurmes," 1862, p. 118.

[2] *Archiv f. pathol. Anat. u. Physiol.*, Bd. xlvii., p. 370, 1869.

[3] The statement of Moniez (*loc. cit.*, p. 143) that the vascular network of the head opens externally on the lips of the suckers by a large number of small oscula, requires corroboration. The "ampoules pyriformes," as the oscula are designated, recall the "doubtful bodies," perhaps unicellular glands, previously described (p. 678).

and development of the yolk-glands, peculiarities are to be observed which never occur in the *Tæniæ*, and which prove this tape-worm to belong to a markedly divergent group of Cestodes. The same characteristic distinctions obtain, with more or less uniformity, in the related species of *Bothriocephalus*, and especially in the larger forms which are found in mammals.[1]

We have already outlined the steps in the historic growth of our knowledge of these peculiarities, nor shall we do more than recall that it was not the nearly related parasites which supplied the basis for the distinction and definition of the species under discussion, but the large-jointed *Tæniæ* of man.

The Genital Apertures and their surroundings will first occupy us in describing the reproductive system in detail.

A first glance at a ripe adult joint seems only to reveal two genital apertures. Situated one behind the other, separated by a short distance (0·3-0·4 mm.), varying slightly with the state of contraction, these apertures lie in the middle region of the ventral surface, somewhat approximated to the anterior margin of the joints. They are usually found, as Eschricht reports, on the posterior limit of the first quarter of the joint, yet cases may be observed where they have been displaced by the state of contraction, either further forwards or backwards. Even Linné observed these two openings, but thought erroneously that they occurred only in certain specimens (his *Tænia vulgaris*), and that in others (*T. lata*) only a single aperture was present.

The anterior opening is seen on closer examination to be the male. It is larger than the one behind, and forms usually a gaping transverse cleft, from 0·25 to 0·34 mm. broad, the upper lip of which is protruded outwards by the cirrhus-pouch which lies above it. The penis is sometimes seen projecting as a small filamentous appendage. The second, also transverse, aperture, which serves for the exit of the ova, is scarcely half as broad as the upper, but is also somewhat raised, so that the whole area surrounding the genital apertures almost always protrudes in the form of a slight elevation. In fresh specimens this protruding area is readily recognisable through its whitish colour, which is due, not wholly and exclusively to the subjacent tissue, but also to numerous small papillæ, which occupy

[1] See on these forms Krabbe, "Recherches helminthologiques en Danemark et en Islande," Copenhagen, 1866, pp. 27-39. The various species are somewhat difficult to distinguish, but I think I am warranted, on the strength of repeated investigations, in affirming that in the organization of the reproductive system, and especially in the structure of the uterus, in the character of the papillary area, and in the disposition of the yolk-glands, differences obtain among them not less than those which distinguish the large-jointed *Tæniæ*.

the area, and are specially closely grouped between the openings. On microscopic examination they are seen to be conical elevations

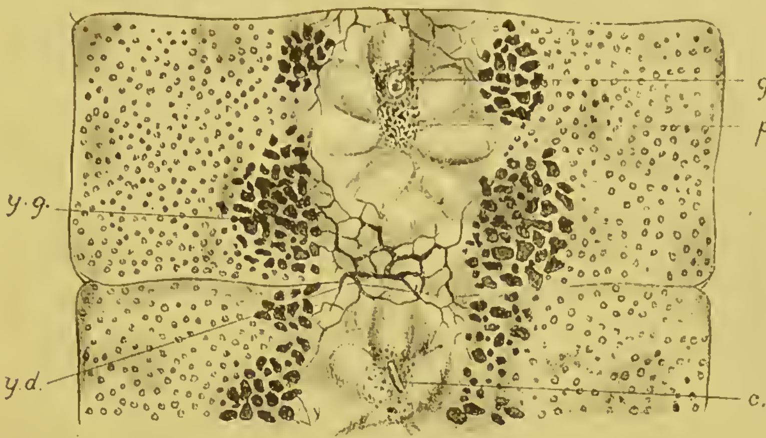

FIG. 362.—Mature joint of *Bothriocephalus latus*. *g.*, genital apertures; *p.*, papillary organs; *y.g.*, yolk-glands; *y.d.*, "yellow ducts"; *c.*, cirrhus protruded (after Eschricht). (× 8.)

of the cuticle (0·02 mm. high, 0·03-0·04 mm. broad), which enclose in their basal portion a single or double (rarely triple) clear, nuclear, or knob-like body. Although Eschricht, who described these structures quite correctly, and indeed better than his successors (till Stieda),[1] believed they were cutaneous glands, we shall probably not be far astray in regarding them as tactile papillæ.

If the anterior genital opening be more closely examined, and that preferably and most satisfactorily in longitudinal sections through the papillary region, it does not require long to be convinced that the former does not by any means solely belong to the male apparatus. At the base of the opening one can see, close behind the aperture of the cirrhus-pouch, a second smaller opening, which was discovered even by Eschricht, although he was unable to determine its true nature. He suggests the possibility that it leads into the anterior loops of the uterus, yet he had not any doubt that the opening further back was to be regarded as the *os uteri*.

Through the observations of Stieda, we have attained to a clear conception of the nature of this second aperture, adjacent to that of the cirrhus. We know now that it (Fig. 363) is the aperture of the vagina, of a duct which was already seen by Eschricht, and subsequently by Böttcher, who defined it as the vagina, though both made the mistake of maintaining its connection with the opening of the uterus.

[1] Braun has overlooked former descriptions of this papillary area, and regarded himself as its discoverer, *loc. cit.*, p. 42.

We have already seen the importance of this discovery of the vagina and its aperture for the right understanding both of the morphology and physiology of the reproductive organs of *Bothriocephalus*.

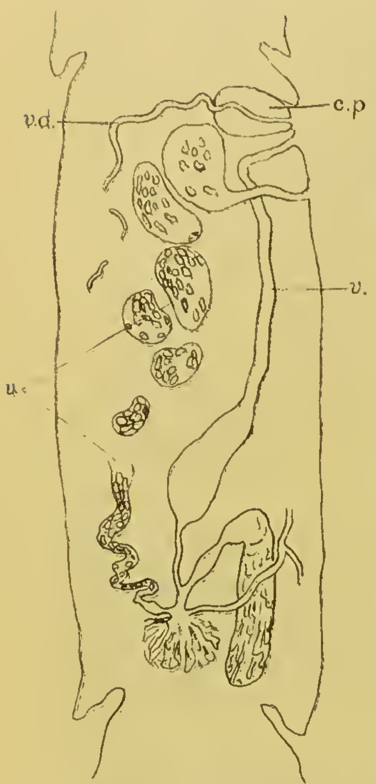

Fig. 363.—Longitudinal diagrammatic representation of the three generative ducts in their connection with the the genital apertures and with one another. *v.d.*, vas deferens; *c.p.*, cirrhus-pouch; *v.*, vagina; *u.*, uterus.

Since the vaginal aperture, as above noted, lies at the bottom of the anterior genital opening, which also includes the opening of the cirrhus-pouch, and was till Stieda's discovery described as simply the male aperture, there is a certain justification for speaking of a sexual cloaca in *Bothriocephalus*. It must, however, be kept in mind that this cloaca is in nowise to be associated with the structure of the same name in the *Tæniæ*. While the latter, in virtue of its depth and narrow aperture, appears as a morphologically independent structure, which does not alter its form or character even when the penis is protruded, the cloaca-like cavity in the form under discussion is different, inasmuch as, on protrusion of the penis, it is more or less completely smoothed out by the retraction of the lips; and that so far that the vaginal aperture comes to lie exposed on the surface of the joint, below that of the cirrhus, in a situation which in other species is the persistent one, *e.g.*, in *B. maculatus* of the leopard and lion, where there is almost no genital cloaca. This being so, it is perhaps more correct to regard the genital pore of this worm as the result of simple invagination, as Eschricht had indeed done in designating the lip-like marginal swelling the "præputium."

The Cirrhus, when protruded, is seen as a slender cone (Fig. 362), not unfrequently protruding half a millimetre, or even more, out of the genital aperture. It has accordingly a much more considerable size than in the cystic tape-worms, in which (*T. saginata*) it is hardly ever larger than 0·18 mm. At its base it measures in the present species fully 0·1 mm., which is more than double its measurement at the end. The canal which penetrates it, and opens at its apex, collapses in the empty state, but is not unfrequently filled with spermatozoa, and then occasionally measures as much as 0·02 mm. or more.

In spite of its considerable size, the cirrhus of *Bothriocephalus* is nothing more than the externally evaginated anterior portion of the

cirrhus-pouch. As such it consists mainly of connective tissue, and that of the very vesicular kind which we have already found in the matrix of the worm.

The Cirrhus-Pouch can only be adequately studied by the method of sections. From superficial preparations merely, only an imperfect survey of the arrangement can be obtained. In such the cirrhus-pouch simply appears as a roundish disc of considerable size (0·4-0·44 mm.), which lies superiorly behind the porus genitalis, and extends to the anterior margin of the joint. This disc is seen on close examination to be the optical section of a hollow muscle, which has when quiescent a somewhat regular oval form, and is inserted on the ventral surface of the joint, *i.e.*, on the porus genitalis, usually with an anterior angle of from 75° to 80°. The posterior pole of the pouch usually lies higher than the porus genitalis, but is, in consequence of the considerable length of the pouch (0·5-0·55 mm. in the ripe joints), so nearly approximated to the dorsal wall, that it is only separated by a small interval (0·01 mm.) from the dorsal transverse muscle-bands. The opposite ventral pole is different, since it penetrates the transverse muscle-sheath and the whole cortical layer as far as the subcuticula; and the latter has also but a slight thickness where it lies above the pouch.

FIG. 364.—Transverse section through the body of *Bothriocephalus latus* at the level of the cirrhus-pouch. (× 10.)

The canal which penetrates the cirrhus-pouch is a direct continuation of the seminal duct, and is morphologically nothing but its terminal portion. Its peculiarities are secondary adaptations to copulatory functions. Apart from the musculature which surrounds it like a bulb, its peculiarities consist especially in this, that instead of pursuing a straight course, it is rolled up in close spiral coils. This is especially true of that portion of the duct which penetrates the (dorsal) half of the bulb, and which, being always filled with semen, serves as a sort of seminal vesicle. The portion further forward is simpler; the spiral coils are disposed in a less extensive zigzag (Fig. 361). Only the outermost portion opening freely at the end of the cirrhus-pouch exhibits an almost straight course. It is this anterior, partly stretched, partly zigzag, twisted portion of the seminal duct which is evaginated by the muscular pressure of the cirrhus-pouch to form the cirrhus. It differs histologically from the posterior portion

only in so far as it is internally clad by a somewhat firm, doubly contoured cuticle, which is continued at the outer openings directly into the cuticle of the cloaca, and like it rests on a distinct subcuticular layer of cells. This can hardly, of course, be compared with the subcuticular layer covering the body. It has but an insignificant thickness, and gradually vanishes posteriorly towards the seminal vesicle. Like the latter, this zigzag coiled posterior portion of the canal is usually filled with semen, and much widened, while the extended terminal portion remains always empty and closed.

The cirrhus-pouch, which surrounds the above-described canal like a bulb, protrudes the anterior portion of the cirrhus, and thus brings about copulation. The muscles admit of simpler and sharper analysis than in *Tæniæ*, and are evidently disposed for the discharge of this function.

The external wall (Eschricht's "capsule") is formed of a thick sheath of muscles, whose fibres, as Landois and Sommer rightly observed, generally run in the longitudinal direction of the bulb, extending from the rounded dorsal pole to the genital pore. Near the latter they bend for the most part from their former direction, mingling with the adjacent longitudinal fibrous bands, and ramifying in the cortical layer. By the contraction of these fibres the cirrhus-pouch is pressed diagonally downwards against the yielding floor of the cloaca, so that the latter is arched outwards, and the inferior segment of the bulb protruded like a plug. The canal is not, however, evaginated without the pressure of the circular fibres, which lie partly isolated among the longitudinal and partly united in plexiform fashion, penetrating (in the anterior half of the cirrhus-pouch as far as the evagination occurs) even into the deeper connective-tissue masses, and being thus eminently capable of affecting these. Under the pressure of the circular fibres the inferior pole of the pouch assumes first of all a mammiform shape, until, through the evagination of the enclosed canal, whose lips represent the *pars minoris resistentiæ*, the cirrhus proper is subsequently protruded. It need not be specially mentioned how during this operation the coils of the canal are unwound and the spiral turns of the posterior portion straightened.

Not only the protrusion of the cirrhus, however, but also its retraction, is fitly secured by radial fibres, which spring on every side from the muscular envelope of the cirrhus-pouch, penetrating the cortical substance at varying intervals, finally uniting with the external wall of the pouch, that is, with its subcuticular layer. The cirrhus-pouch has its own special retractor muscles, in the form of sagittal fibres, which pass from the dorsal surface of the joint, and are inserted on the adjacent segment of the muscular capsule.

The thick layer of annular fibrils, which surrounds the coils of the seminal duct, effects probably only the forward movement of the internal seminal mass, forcing it into the cirrhus.

That the cirrhus is really a copulatory organ is, in spite of Landois and Sommer's contradiction, all the more certain since the sensory papillæ on the genital area point clearly to a sexual association of the joints; but this is still far from having been verified by observation.

The Vas Deferens is directly continuous with the canal within the cirrhus-pouch, as has been described above, and the cirrhus-pouch itself is a muscular apparatus developed round about it. One might therefore readily suppose that the entrance of the vas deferens into the pouch coincided with its distal pole, as its aperture does with the proximal. Such is not, however, the case. The entrance of the vas deferens occurs rather at the portion turned backwards, towards the hinder border of the joint, and at a considerable distance from the end of the cirrhus-pouch, so that the latter arches above it in the form of a hemispherical protuberance, while the spirally coiled canal within forms in its windings an arch open posteriorly. It is of course only the quiescent state of the cirrhus-pouch which exhibits this appearance, for with the protrusion of the cirrhus the cæcally projecting portion of the pouch undergoes a reduction, in consequence of which the insertion of the vas deferens becomes apparently altered.

Just at its point of entrance into the cirrhus-pouch the vas deferens is further surrounded by an ovoid bulb, which, though of course much inferior in size, rarely measuring more than 0·2 mm. long by 0·4 mm. thick, undeniably recalls the structure of the cirrhus-pouch by its muscular character, and by the coiled course of the canal within it. There are indeed many differences in detail. Not only is the connective tissue much less developed in proportion to the muscular tissue, but the latter seems to be somewhat differently disposed, since the radial muscles are absent, and the others are united in a close web, whose fibres extend for the most part annularly, partly, however, crossing one another diagonally. Longitudinal fibres are only present in small numbers.[1] It can hardly be doubted that this muscular bulb serves to force into the cirrhus-pouch the semen which frequently collects in considerable quantity within the canal.[2] According to Böttcher, it simply represents a seminal vesicle.

The vas deferens is seen as a highly coiled canal, extending on

[1] I could not see the strong cilia which Moniez (*loc. cit.*, p. 144) found within the bulb, and which had a distinctly cellular character ("les cils sont volumineux, leur nature cellulaire ne peut être mise en doute"). Nor could I perceive the cilia in the vagina which he has described (*ibid.*, p. 148).

[2] Eschricht overlooked this apparatus, for the citation by Stieda and others to the

the dorsal surface of the uterus, the loops of which it accompanies in more or less close apposition (Fig. 365), but on the whole the bendings which it exhibits are smaller and less ample. There is an obvious difference here between the present species and the *Tæniæ*, and this is further emphasised by the fact that the vas deferens in this worm is not only considerably wider, but also bears a sheath of circular muscle fibrils, which, like the bulbar swelling at the upper end, serve to force forward the enclosed spermatozoa. According as the number of the latter is large or small, the width of the canal varies, increasing sometimes from 0·035 mm. to double that and more, besides exhibiting, at certain places, considerable varicose swellings. This is seen most strikingly and most frequently at the lower end, which, being filled with semen, not unfrequently forms a conspicuous "seminal cistern" (Landois and Sommer), shining through the first coils of the uterus, just in front of the ovary, in the form of a darkish, saccular, irregular body, sometimes measuring 0·2 mm. in thickness. The sperm mass is brought into this receptacle by the afferent canals, which in a variable, but always limited, number lead into the "cistern" from right and left, and connect it through their much ramified lateral branches with the testicular vesicles. The irregularity in the number of afferent ducts is due for the most part to a very early bifurcation. I have seen joints in which the lower end of the vas deferens divided into two limbs, which extended almost at right angles into the lateral areas, there to ramify further, and also others in which, on either side, three or four collecting ducts led into the "cistern." The branches of the collecting ducts, or the ducts themselves when several occur, are directed both backwards and forwards. Nor are they by any means confined to the area of the joint to which they really belong, but extend beyond the boundaries, coming into connection with the superior testicular vesicles of the following joint.

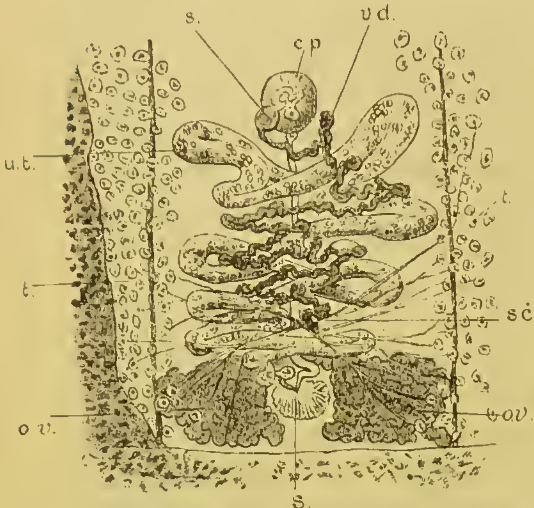

Fig. 365.—Male generative organs of *Bothriocephalus latus*, seen from the dorsal surface; *c.p.*, cirrhus-pouch; *s.*, swelling adjacent to it; *v.d.*, vas deferens; *s.c.*, seminal cistern; *t.*, testes; *ut.*, uterus; *s.g.*, shell-gland; *ov.*, ovary. (× 20.)

contrary refers to a second small vesicle within the cirrhus-pouch (*loc. cit.*, p. 50), and cannot apply to the appended bulb. The latter was first discovered, described, and explained by myself.

The more the ramification progresses, the thinner and more delicate do the twigs become, until they finally escape detection. Only in isolated cases can they be seen uniting with the testes (which then appear stalked), and especially with those which lie nearest the median area. They have, as a rule, a comparatively straight course, and frequently seem, especially near the seminal cistern, to result from a dichotomous branching.

The Testes themselves exhibit exactly the same structure and disposition as in the large-jointed *Tæniæ*. The vesicles have a similar irregularly oval or spherical form, and have when full-grown an average diameter of 0·1-0·13 mm. They extend in a thick layer over the lateral portions of the middle layer (Fig. 361), and are here and there insinuated between the loops of the uterus. Towards the lateral borders they are more closely grouped, and the transverse diameter becomes diminished in consequence. Stieda has estimated their number at about 320-400 in each joint, while Landois and Sommer compute it at 1000-1200. According to my estimate, the former is below, the latter above the mark. In each lateral area I count twenty-three in a transverse line, and sixteen in a longitudinal, and thus compute a total of between 600 and 700, which agrees well with Eschricht's estimate of 700.

Both Landois and Sommer and Moniez describe the testes as simple lacunæ in the tissue of the middle layer, but with reagents I can distinguish the coagulated contents from a distinct, delicate, enveloping, cuticular membrane. The striated substance within the mature vesicles consists of extremely fine long spermatozoa, which are grouped in numerous bundles, or rolled up, and which (according to Stieda and Sommer and Landois) bear at one end a strongly refringent head. Between these can be seen separate aggregates of small (0·005 mm.) nuclear cells (Kernzellen[1]), which occur in much greater abundance in the unripe vesicles, where they may, indeed, form the whole contents. It is hardly necessary to remark that these cells in course of time develop into spermatozoa. Their occurrence in the ripe testes also shows that the formation of spermatic elements in *Bothriocephalus* is not, any more than that of the ova, restricted to a definite period, as in the *Tæniæ*, but continues as long as the vegetative life of the joints.[2]

The dark balls which not unfrequently occur in the ripe joints between the coils of the uterus and of the vas deferens, are, in spite of

[1] Deceived by these cells, Bötticher (*loc. cit.*, p. 121) thought that each sperm-filled testis was a coil of fine canals, with an internal cellular lining.

[2] According to Moniez, the spermatozoa are formed freely in the tissue of the tapeworm, roll themselves up in spherical masses, and make their way independently to the ramifications of the vas deferens (*loc. cit.*, p. 147).

their considerable size (up to 0·25 mm.), to be regarded as degenerated testicular vesicles. This supposition is at least more probable that the interpretation of Landois and Sommer, according to which they are "portions of the vas deferens or of the large seminal ducts" which have been constricted off, and whose contents have undergone fatty metamorphosis.

The Female Reproductive Organs.—The Vagina, as above noted (Fig. 363), opens just below the cirrhus-pouch into the bottom of the genital cloaca. In spite of the approximation of their apertures, their mutual position is such that the possibility of self-fertilisation seems all but excluded. For such a purpose the cirrhus would have to bend at an acute angle backwards and downwards, for which it is the less capable, since the cloaca is flattened out when extruded, and external pressure cannot therefore act upon it, as in the *Tæniæ* (p. 309).

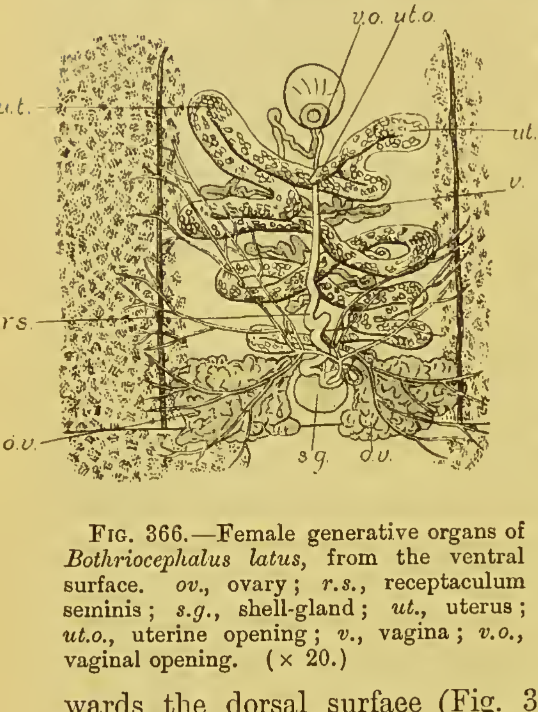

FIG. 366.—Female generative organs of *Bothriocephalus latus*, from the ventral surface. *ov.*, ovary; *r.s.*, receptaculum seminis; *s.g.*, shell-gland; *ut.*, uterus; *ut.o.*, uterine opening; *v.*, vagina; *v.o.*, vaginal opening. (× 20.)

The vulva is a somewhat wide (0·06 to 0·085 mm.) and funnel-shaped, but yet short, invagination of the external envelope of the body, which is directly continued into the much narrowed vaginal canal (0·024 to 0·04 mm.). The latter extends, as can be seen in longitudinal sections, for some distance below the cirrhus-pouch towards the dorsal surface (Fig. 367). It bends, however, before it reaches the opening of the vas deferens, at an acute angle towards the ventral aspect, and finally extends almost straight backwards, in the middle line, upon the transverse muscle layer of the joint. Reaching the anterior border of the ovary, it leaves the ventral muscle-layer, passing on to its dorsal surface, on which it continues its course for some distance further. The posterior end of the vagina usually forms a more or less large (0·12 to 0·2 mm.) saccular dilatation, filled with semen. This is to be regarded as a receptaculum seminis, although it is not in any way histologically different from the rest of the canal, and is further so slightly separated anatomically, that when quite filled it is for some distance quite continuous with the adjacent portion of the canal. This cæcal vaginal receptacle communicates by a narrow duct, as we shall presently see, with the hinder end of the uterus and with the other portions of the female apparatus.

The most important histological character of the vagina is the presence of a muscular layer consisting, for the most part, of circular fibres, which begins at the base of the vaginal entrance, and acquires a specially strong development in the dilated sac. The internal lining of the canal is formed of a thin, but sharply defined cuticle, which is continued at the vaginal opening into the cuticular covering of the body.

It was only after the discovery of this vagina that it became possible to homologise the structural relations of the reproductive organs in *Bothriocephalus* with those of the *Tæniæ*. We know now that in the former as well as in the latter the uterus serves only for the reception of the ova, and the difference between it and the *Tæniæ* is thus essentially reduced to this, that the uterus is not closed, but has an opening through which the ova pass outwards.

FIG. 367.—Diagrammatic representation of the course and connections of the vagina, as seen in longitudinal section. *v.d.*, vas deferens; *c.p.*, cirrhus-pouch; *v.* vagina; *ut.*, uterus; *ut.o.*, uterine opening; *f.c.*, fertilising canal; *o.d.*, oviduct; *s.g.*, shell-gland.

The Uterine Aperture, as has been already described, is seen a short distance (Fig. 367) behind the genital cloaca, at an interval of between 0·25 and 0·4 mm., according to the state of contraction of the segment. It is surrounded by margins which are but little swollen, has a width of 0·15 mm., and, rapidly narrowing, leads into a canal (of 0·04 mm. in diameter) which is inserted at right angles to the ventral surface, penetrates the cortical layer, and then somewhat suddenly widens into the upwardly directed first coil of the uterus which lies right or left of the cirrhus-pouch.

The Uterus, whose true structure was first recognised by Eschricht, consists of a simple coiled canal, which extends from behind forwards in the internal layer of the joints, and at the height of its development occupies the greater part of the whole median portion. The windings extend alternately right and left across the middle line, and the adjacent bands of their loops at first suggest the lateral processes, which we have already seen in the large jointed *Tæniæ*. On closer examination, however, this resemblance is seen to be an illusion,[1] and

[1] Bötticher's statement that a direct connection exists in the middle line between the loops which here cross each other is based on a misinterpretation.

that most distinctly in undeveloped or only half-developed joints, in which the course of the uterus can often be followed throughout its whole extent. It is only when the ever-increasing mass of ova gradually distends the canal, when the limbs of the loops become not only longer but broader, partly overlapping one another, that the uterus assumes the form of a "rosette," or of a "heraldic lily," which was regarded by the older helminthologists as the most important distinctive character of the species.

The number of loops, or of "horns" as they are usually, but inaptly, designated, is in *Bothriocephalus* usually five (four to seven) on either side. When fully developed they possess a width of about 0·5 to 1 mm., and a length of about 2 to 2·5 mm., so that the total length of the uterus is usually between 25 to 30 mm. The anterior

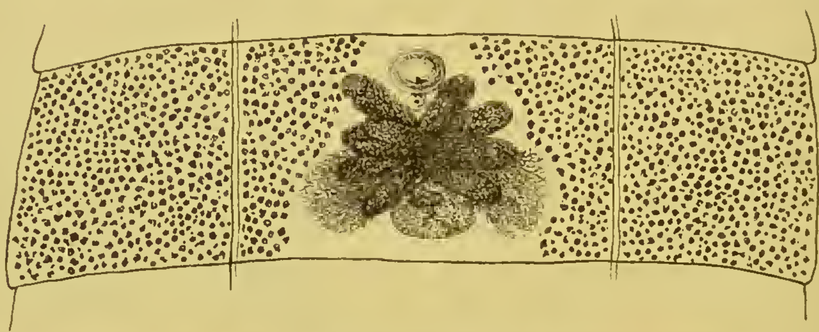

FIG. 368.—Ripe joint of *Bothriocephalus latus* with the uterine rosette. (× 6.)

horns, though not always the longest, are pretty generally the thickest, and in the older joints are usually distinguished from the others by a dark colouring. They are situated at the sides of the uterine opening and of the cirrhus-pouch, on either side of which they diverge upwards, while the middle horns usually exhibit a more transverse course, and the posterior generally diverge backwards. So it is at least when the joints are somewhat strongly contracted. With the increase in length, the various loops shorten and separate somewhat from one another. In assuming a more parallel disposition, the above noted resemblance to the joint of a *Tænia* becomes more marked and deceptive, but the absence of a marginal pore prevents the possibility of confusion. The other structures are also affected by the extension, as is shown by the fact that the marginal space free from ova, and especially in front, is in such cases disproportionately large.

One might be inclined to attribute the looped arrangement of the uterus primarily to the accumulation of ova in the uterus. Such is not, however, the case. The loops may be observed even in imperfect development, at a time when no ova are present in the uterus. They are rather the expression and result of a growth in length,

which is disproportionate to the length of the joint. It is different with the width of the uterus, which increases in proportion as the eggs accumulate within it. At first so narrow that the ova can only lie singly, it continues to grow, till eight, twelve, fifteen, or even more can find room beside one another. It is thus easily explained how the lumen of the uterus is so narrow as it is in young joints, and in the lower loops, even when the joints are mature.

The wall of the uterus is formed of an apparently very extensile and structureless membrane, the independence of which may be clearly seen in the narrower loops, but which with increasing width becomes continually more delicate and less readily separable from the surrounding connective-tissue. An epithelium, such as Stieda and Moniez report, is not present, but after hardening, one can not unfrequently detect on the inner surface of the cuticle the finely granular residual traces of the ova. This finely granular substance occurs also between the eggs, and is probably an unused remnant of the yolk.

The cuticular coat of the uterus is externally surrounded by a cellular layer, whose constituent elements are distinguished from the ordinary connective-tissue cells by their abundant protoplasmic contents, by their smaller size, and by their close grouping. In their appearance and form they sometimes recall the subcuticular cells. In the only moderately distended portions of the canal, they are less sharply defined than in the wider parts, and are so abundantly developed that Eschricht actually regarded the sheath formed by them as a special organ (the capsule of the uterus). Special musculature is only recognisable on the narrowed tubular portion of the uterus, which connects the last loop, lying to the right or left of of the cirrhus-pouch, with the female genital aperture. It consists of a layer of circular muscles, which embrace the canal, and have the effect of forcing the contained ova outwards. One not unfrequently finds single ova still lying within the funnel-shaped opening. Their transmission into this expelling apparatus, like the forward movement through the uterus, is, apart from the *vis a tergo*, effected by the pressure of the body-muscles, and especially by the sagittal fibres which extend between the coils of the uterus, and approximate the two surfaces of the joint.

Special attention must be devoted to the posterior end of the uterus, which extends behind the rosette, and is formed of a coiled canal, becoming ever narrower and more delicate the further it extends. The upper coils appear as comparatively regularly alternating loops (Fig. 368), but shorter and thinner than those of the rosette; inferiorly, however, the windings become more irregular in

their course, so that Eschricht described them as a special structure, the so-called "knot." The canal of this coil usually contains only a single row of ova, including, however, also numerous free-yolk granules, which indeed are so abundant that the coil acquires thereby a more or less dark appearance. This is especially true of the outer end of this coil-tube, which has usually the form of a spindle-shaped sac (0·06 mm.), lying sometimes to the right, sometimes to the left of the middle line, and which is the portion of the uterus where the eggs acquire their hard shell. This is due to the fact that the terminal portion not only receives the above-mentioned (p. 701) fertilising canal, but also communicates with the efferent ducts not only of the ovary and of the yolk-gland, but also of the shell-gland (Fig. 366).

The observation of this terminal portion is exceedingly difficult, and the reports of investigators differ considerably as to its relations. My enquiries have led me to conclusions which agree most closely with those of Sommer and Landois; the differences of opinion being chiefly on subordinate points. They concern only the mode of connection between the different portions, that such a connection does exist, and that it is effected by the terminal portion of the uterus, has been allowed by all observers since Eschricht.

The Fertilising Canal will first be considered; as we know it extends from the dilated lower end of the vagina (the receptaculum seminis), and which has the function of supplying the uterus with the semen necessary for the fertilisation of the ova. For this purpose this canal affords direct communication between the receptaculum and the terminal portion of the uterus. It is a comparatively short duct, which describes in the median plane of the joint a curve open anteriorly. The longer limb, which descends on the ventral side, and first receives the semen, has only an inconsiderable thickness (0·015 mm.), so that it is sharply and definately separated off from the receptacle. Sommer and Landois have described it—it seems to me erroneously—as extremely delicate, since a muscular sheath is distinctly recognisable. It is internally lined by a relatively compact cuticular membrane. Before this descending limb reaches the point where it bends round, it receives the common oviduct, just as we have seen (p. 445) in the fertilising canal of *Tænia*. At the same time it widens, so that Sommer and Landois regard it thenceforward as a direct continuation of the oviduct. Shortly after receiving the latter, the fertilising canal describes the above-mentioned loop-like bend, and becomes again narrower, until after a short course it passes into the terminal portion of the uterus, which is dilated again here.

The Shell-Gland communicates with the uterus at the bend above referred to. It has the form of an ovoid or spheroidal body of considerable size (0·4 mm.), and is seated on the convex margin of the bend. In transparent preparations it can be seen even with the unaided eye. It lies in the middle line, below the uterine coil, just before the posterior margin of the joint, at a position, therefore, where the yolk-gland is situated in the *Tæniæ*. This fact contributed not a little to the mistake I made in the first edition of this work, in identifying the two structures, and in regarding the shell-gland of *Bothriocephalus* as the ovary, under the erroneous supposition that the yolk-gland of the *Tæniæ* produced the eggs. Nor did the histological structure of the body seem so decidedly against my opinion, for Böttcher, and at first Stieda also, supported the same interpretation, although they both had already recognised the true ovaries in Eschricht's "lateral glands." They believed that the shell-gland, which had been also described by Eschricht as the "knotted gland," and regarded by him as probably serving for the secretion of albumen, was the median portion of the ovary. In the appendix to his first contribution, Stieda, however, recognised the true nature of the body.[1]

FIG. 369.—Female reproductive organs of *Bothriocephalus latus*, seen from the ventral surface. Between the two ovaries is seen the shell-gland. (× 20.)

The parenchyma of the gland consists of a large number of pear-shaped cells of 0·02 to 0·025 mm., enclosing clear or slightly turbid contents, and each drawn out into a thin duct of considerable length. The ducts are all directed inwards, and after a more or less straight course, are all separately united with the loop of the fertilising canal.

It is not strictly correct to speak of this complex mass of unicellular glands as a spherical body, for not only is the centre of the mass which is penetrated by the efferent ducts formed of ordinary connective tissue, but there are no glandular cells on the

[1] Moniez has lately reproduced the old mistake. He regards the shell-gland as a special median portion of the ovary ("ovaire central"), in which, however, the ova never attain maturity, but become abortive. Only the lateral ovaries produce eggs. After liberation, they pass into a cavity in the parenchyma between the ovaries, are received in the adjacent funnel or trumpet-like muscular end of the oviduct ("pavillon de l'oviducte"), and passed onwards. The fertilising canal and oviducts are not united with the uterus till some distance from the uterine receptacle.

anterior portion, nor where the fertilising canal joins, so that the true shape is rather that of a very bulging goblet, open superiorly.

The Ovaries are, as in reality even Eschricht knew, and as is now indubitably demonstrated, the so-called "lateral organs," two wing-shaped structures of considerable size, which (Figs. 368 and 369) include the shell-gland and the knotted-gland between them, and ascend on the outside of the lower loops of the uterus. The lateral portions extend to some distance beyond the median area, and the posterior extremities can usually be traced close to the margin of the joint.[1] Like the ovaries of the Tæniadæ, which they resemble in form, these organs form a flat, glandular body, closely apposed to the musculature of the ventral surface, and composed of numerous long, ramifying cæca, spread out one beside another. This is best seen in injected preparations, where the cæca are distinctly evident, in spite of Moniez's denial.[2] The tubes have a thickness of about 0·03 to 0·04 mm., and extend in thick and short serpentine twists, so that they appear as if sinuate. Especially in the upper half, where they lie more closely and frequently overlap, the appearance of a composite network is suggested. In such cases the course of the tubules can rarely be followed for any distance, nor can their disposition be definitely determined. We may, however, generally describe them as radiating out in a fan-like fashion from above and from within, as is especially corroborated by the fact that the lateral organs are connected by a transverse bridge, extending in front of the lower end of the receptaculum seminis. The structureless membrane which bounds the tubules and this bridge externally is continued in the middle line of the joint into the proper oviduct, which extends backwards in a straight or slightly curved course, between the receptaculum and the ventral musculature, increasing gradually in width from 0·01 mm. to more than twice that, and finally opening, as above mentioned, into the fertilising canal (Fig. 367).

The ripe ova, which are met with especially in the bridge-like connecting portion, appear as pale, membraneless balls, measuring 0·018 mm. in diameter, enclosing a vesicular nucleus of 0·009 mm., within which a nucleolus of 0·003 mm. can be seen. They are considerably smaller in the ovarian tubules, especially towards the

[1] I have never observed that, as stated by Sommer and Landois (*loc. cit.*, p. 20), they extend beyond the posterior margin, as a flat ribbon-like appendage, reaching into the next joint. Such an appearance was, indeed, occasionally seen, but a closer examination showed that it was due to the overlapping of the margin of the joint.

[2] Moniez denies the existence of special ovarian tubules, interpreting the appearance as strands of ova, embedded without envelope between the connective-tissue cells. The eggs are said to be like those of the Cestodes generally, simply modified cells of the surrounding tissue (*loc. cit.*, p. 156).

end, where they sometimes measure only 0·006 mm. (nucleus = 0·0045 mm.).

The ova pass from the oviduct into the commencement of the uterus through the fertilising canal, in which they acquire their final form by being equipped with yolk and shell. The fertilisation probably takes place previously, during the passage through the fertilising canal, as I conclude from the fact that I was but rarely able to discover spermatozoa within the uterus.

The yolk-spheres, which surround the ovarian ova in large numbers (from 25 to 30), are seen to be also membraneless nucleated cells, having, however, a decidedly smaller size (at most 0·01 mm.), a smaller nucleus (0·004 mm.), and a plasma containing numerous fine and coarse granules. Eschricht correctly recognised the seat of formation of these spheres in the so-called "granular heaps," which, with their efferent apparatus from the yolk-gland of *Bothriocephalus*, may be most fitly termed "yolk-vesicles."

As already noted, these structures belong to the cortical layer, in which they extend in a simple close-packed layer beneath the subcuticula (Fig. 361). They are found both on the dorsal and ventral surface, but only in the lateral areas, the median region remaining for the most part free. The yolk-vesicles in the middle area, especially on the ventral surface, are, however, considerably larger than those more peripherally situated, some of which do not measure more than 0·04 mm., while the former are sometimes six or eight times as large, so that they become recognisable by the unaided eye, especially since their contents render them non-transparent. The other yolk-vesicles are, of course, also non-transparent, but in consequence of their small size, this is only expressed by the darker shade of the lateral areas in which they are situated. In their form they somewhat recall the testicular vesicles, with which Küchenmeister long regarded them as identical. The contents and situation are, however, quite different, as also the closer disposition, so close in some places that the spheres coalesce. In longitudinal sections I count, like Stieda, about thirty of these in transverse section, about forty-five to fifty on each side on the dorsal and ventral aspect, so that the total number in each joint must be near 6000, as Eschricht also estimated. No special membranous boundary is recognisable. They are simply collections of cells and granules, but the former have not from the first, especially in young joints, their subsequent size.

Since the yolk-vesicles are destitute of distinctly independent boundary, their contents can only be expelled by the contraction of the body-muscles. Especially the sagittal fibres are concerned in this action, for they extend between the vesicles which owe to them

their form, usually ovoid, and somewhat produced inwards. The external portion protruding between the subcuticular cells is thus often drawn out into a conical point, which at the first glance suggests the presence of an opening, which has been maintained by some observers. Contrary to appearance, however, the expulsion of the contents takes place at the end turned inwards, and that by means of a duct, which is indeed only recognisable when it contains yolk, which is by no means always the case. At first narrow and inconspicuous, perhaps even without a distinct wall, these ducts gradually unite to form canals, which extend between the yolk-vesicles and the longitudinal muscular sheath, and finally develop into a system of tubes, often conspicuous (even under a low power) on the ventral surface, because of their contained yolk and wide

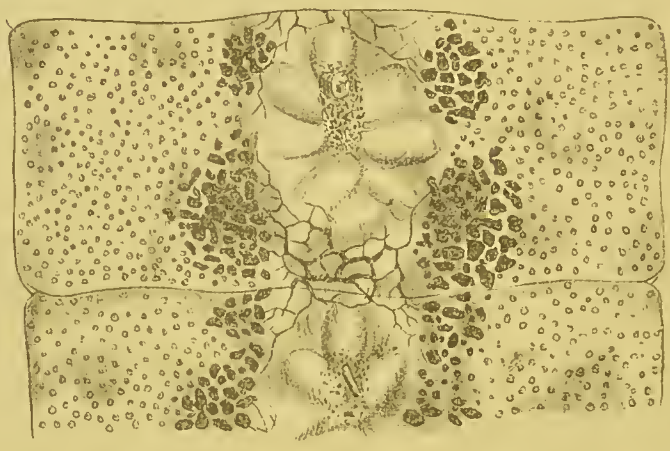

FIG. 370.—Segment of *Bothriocephalus* with yolk chambers and "yellow ducts," after Eschricht. (× about 8.)

extent. Eschricht even recognised this efferent apparatus, and connected it with the "granular heaps," although he, under the influence of Ehrenberg's polygastric view of the Infusoria then in vogue, was at first inclined to regard the latter as stomachic sacs. The "yellow ducts," whose discovery so excited Eschricht that he could hardly wait for the daylight in his anxiety to see them again, are nothing more than the branches of this efferent apparatus, which radiate outwards from the region of the so-called "knot," through the median area, to the lateral portions of the ventral surface. They exhibit sometimes a straighter, sometimes a more coiled course, are at intervals often sinuously enlarged, and exhibit, besides, considerable variety in their degree of repletion. The walls are thin without any histological differentiation, except that in the larger branches a distinct membrane can be recognised.

It is a striking fact, as Eschricht rightly pointed out, that the dis-

tribution of these yellow ducts is not exclusively confined to the joint to which they properly belong, but they extend beyond it into the anterior portion of the joint behind. What we have already emphasised in regard to the vasa efferentia is thus true also of these yolk-ducts—a new proof of the correctness of the assertion that in *Bothriocephalus* the individualism of the joints is much less perfect than in *Tænia*.

The disposition of the efferent ducts on the dorsal surface is much more difficult to follow than on the ventral, yet it seems probable that they are everywhere confined to the cortical layer, and that the ramifications of the yellow ducts never traverse the central layer, but extend along the sides, and in this way pass from ventral to dorsal surface. The only portion of the apparatus which seems to sink into the layer is the unpaired collecting tube, which arises from the union of the yellow ducts at the point whence they radiate outwards, and then extends inwards, penetrating the muscle-layers and opening close in front of the coiled gland (Fig. 371) into the fertilising canal.

FIG. 371.—Diagrammatic representation of the course and connections of the vagina, as seen in longitudinal section. *v.d.*, vas deferens; *c.p.*, cirrhus-pouch; *v.*, vagina; *ut.*, uterus; *ut.o.*, uterine opening; *f.c.*, fertilising canal; *o.d.*, oviduct; *s.g.*, shell-gland.

It is in this way possible that, along with the (fertilised) ova, yolk-cells also pass into the terminal portion of the uterus, and that both kinds of elements become enclosed in a common shell. The material composing the latter is a strongly refringent yellow substance, which is found more or less abundantly in drops between the ova and the yolk-cells. At first these elements all lie near one another, without distinct order or regularity. Soon, however, each ovum becomes surrounded by a number of yolk-cells. They thus become balls of more or less considerable size, which are then pressed against the adjacent drops of shell-substance, so that these become here and there attached to the surface as flattened or watch-glass shaped drops. The subsequent shell arises by the thinning and consequent spreading of the shell-substance over the surface of the balls. While this is going on, the egg has, by further inception of yolk-cells, attained its final size, and the original, often very irregular, form becomes ovoid. Where the lid is afterwards

situated, the shell exhibits for a while a fissure, which is closed at a later stage by the application of a new portion of shell-substance, which always remains isolated. The young shell is brighter and thinner than it subsequently becomes, so that a staining fluid rapidly affects the contents, which no longer happens in the deep-brown older eggs.

Clear and distinct as the processes of oogenesis are in suitable preparations, the actual mechanism eludes observation. It seems plausible, however, that it is the pressure of the surrounding canal which forms the eggs, though the absence of a special musculature in the uterus does not seem to agree with this supposition, nor the fact that the eggs in process of formation do not occur singly, one behind the other, but usually in considerable numbers on the same transverse section. It is possible that special protoplasmic activities (amœboid movements) play some part in the process.

The mature ova exhibit, in form and size, several more or less striking peculiarities, and that quite apart from the not unfrequent occurrence of malformed or stunted specimens. These variations are especially noticeable in the eggs within the lower uterine coils, so that it seems as if they become more uniform the longer they remain within the uterus. In the rosette they have usually a longer diameter of 0·05 mm., and a shorter of 0·035 mm.; but diameters of 0·056 and 0·04 respectively are also not unfrequently present, so that in shape they appear sometimes more elongated, sometimes rounder. The lid is seldom recognisable without pressure to cause it to spring up. It lies at the anterior pole, which is occasionally somewhat flattened, and possesses a diameter of 0·013 mm. (Fig. 359).

What I have noted above in regard to the reproductive organs relates primarily only to the state of the ripe joints, which form, as we know, the great majority in *Bothriocephalus latus*. In a fresh specimen, measuring 720 cm. in length, the number of joints was about 2400. The unripe joints are, indeed, present in considerable numbers (at least 500 to 600). They are characterised by the absence of hard-shelled ova, and afford in their adolescent stages a complete survey of the various stages in the formation of the generative organs.

The Development of the Reproductive Organs commences with an extremely simple structure. It consists, as in the Tæniadæ, of an aggregation of small nucleated cells, occupying the centre of the joint, and but slightly separated from the surrounding parenchymal cells. It is recognisable at a very short distance behind the head, so that it seems probable that the differentiation of these cells has already occurred in the very earliest joints. At first of inconspicuous size,

this heap of cells soon grows into the form of a longitudinal band, while in the cystic tape-worms it extends transversely in correlation with its subsequent structure.

This growth continues for some time without any other modification. In stained preparations of the larger tape-worms (both *Tænia saginata* and *Bothriocephalus latus*) this structure is seen some centimetres behind the head, shining through the cortical layer of the body. In this state the rudiment in *Bothriocephalus* was formerly detected and examined by Eschricht. It seemed at first, however—and with this my account of the rudimentary reproductive organs in *T. saginata* (p. 446) should be compared—as though the rudiment directly formed the efferent apparatus alone, and as though the germ-producing organs originated independently, and became afterwards associated with the former.

Subsequent investigations have, however, convinced me that this opinion is not correct, but that the germ-producing organs also owe their origin to the cells of the primitive rudiment. I can, it is true, affirm this with perfect certainty only of the ovary and yolk-gland of *Tænia*, but the fact that the vasa efferentia, or at least their larger branches, owe their origin to radiations from the vas deferens, suggests that the above statement holds true also of the testes. That the genetic connection between the germ-producing organs and the primitive rudiment is less distinct than that between the latter and the efferent ducts, as is certainly the case, is due to the fact that the latter appear as more massive structures, and exhibit at an early stage a definite boundary.[1]

What I have to communicate with regard to *Bothriocephalus* in this connection is unfortunately very incomplete, and indeed little more than a repetition of the results of Eschricht.

I would first note that the primitive state of the reproductive rudiment persists for some time without marked change. At a distance of about 10 cm. behind the head, the rudiment is still seen as a dark, indistinctly defined, longitudinal streak, extending in the median line of the joints. Three or four centimetres farther back the contours become sharper, and one can detect at the anterior end of the streak, close behind the margin of the joint, a roundish aggregation of cells seated on the others like a sort of head. This structure mainly represents the hitherto incompletely separated rudiment of the genital ducts and the associated efferent apparatus,—organs whose differentiation and formation occupy a length of 15 cm. Fifty centimetres behind the head,

[1] From this one can see how inconsistent it is for Moniez to deny the morphological independence of the germ-producing organs in the Cestodes, and to refer both ova and spermatozoa to the direct modification of ordinary parenchymal cells.

the external genital apertures and the cirrhus-pouch can be distinctly seen. All the efferent ducts extend at first in a straight direction backwards to near the posterior margin of the joint, where the rudiment of the shell-gland and ovary can be distinguished between them. Both originate as appendages and processes of the streak-like rudiment,—the shell-gland at the posterior end, the ovary at a short distance in front of it, extending on either side like a pair of wings. At the same time the testicular vesicles become visible in the median region of the joint. They occupy for the most part the anterior clear portion of the joints, while the yolk-glands, at first small and clear, are to be detected somewhat farther back in the lateral areas.

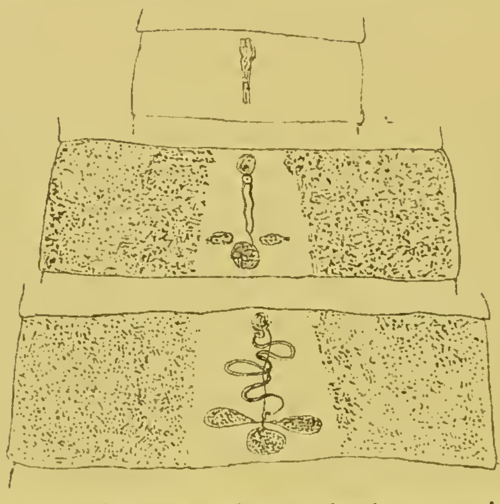

FIG. 372.—Development of the reproductive organs in *Bothriocephalus latus.* (× 25.)

When the various organs have thus been mapped out, they rapidly acquire their full development. Even at a distance of 60 cm. from the head, the uterus, formerly but slightly looped, has, though still empty, acquired essentially its final shape, except that the limbs of the loops are shorter and more distinct than subsequently. Shortly afterwards copulation seems to occur, for a few centimetres farther back a grumous mass, penetrated by spermatozoa and balls of shell-substance, is found in the posterior end of the uterus, and beside this appear the first hard-shelled ova, clear and few in number. For a time the ova lie in a single discontinuous row, but become by further pressure more and more closely aggregated. The width of the uterine canal increases, the limbs of the several loops become approximated, and the appearance previously described is soon exhibited. The more the eggs accumulate the darker becomes the colour of the uterus, and the more distinct its definition. In older joints it appears through the cortical layer as an almost blue, leaf-like lobed mass.

Joints not unfrequently occur in which the external coverings of the uterus have been burst and the eggs liberated; long chains of open or split joints are also occasionally seen. In contrast to the somewhat similar phenomenon seen in the *Tæniæ* (p. 457), this bursting seems here to be due in most cases to a superabundant accumulation of ova within the uterus. The ripe joints of *Bothriocephalus* indeed usually liberate their contents in the normal way—the ova are generally found in large numbers in the fæces of the host—but cases are readily conceivable in which the liberation has not kept pace with the production.

The Abnormalities exhibited by *Bothriocephalus latus* include others than this bursting, which, in consequence of the shortness of the joints, not unfrequently appears as a distinct cleft through a whole series. The doubling of the genital apertures even is quite a common occurrence. I have scarcely examined a single specimen without observing a greater or smaller number of adjacent joints with this malformation. These segments are usually further marked by their form. The limiting margins are not straight, but divided in the middle by a sort of step-like interruption into a right and a left half, which are on different levels. Portions are sometimes even separated by a furrow, which extends from the middle corner of the anterior margin diagonally to the superior corner of the posterior margin. But even where the division is not externally manifest, its presence can be readily detected by the use of a compressorium. A clear line of demarcation in the direction above mentioned is then observable, plainly showing that each half of the joint has its special genital aperture. And more than that, one can see that each of the halves is furnished with a more or less perfect set of genital organs. Most distinct are the uteri, both of rosette-like form as usual, except that the horns directed inwards are distinctly shorter than usual. It may also happen that the two uteri are of unequal size, one having grown at the expense of the other. As with the internal uterine horns, so also the other portions directed towards the middle line are atrophied. One cannot, however, deny that a true duplication has taken place, that there is really a double chain, whose joints have united by their adjacent margins, with concomitant degeneration of the approximated lateral areas. That the joints are wedged alternately into one another is of subordinate morphological importance. This condition is genetically explained, and indeed the whole

FIG. 373.—Series of joints with double genital apertures.

malformation, so far as my researches go, by the interpolation of a half (sometimes only imperfectly separated) joint. This is again repeated, as the adjoining figure shows. The second half joint, of course, belongs to the opposite side.

Occurrence and Development of Bothriocephalus latus.

Knoch, "Die Naturgeschichte d. breiten Bandwurmes mit besond. Berücksichtigung seiner Entwickelungsgeschichte." *Mém. Acad. Sci. St. Petersb.*, t. v., 1862.

Knoch, "Neue Beiträge zur Embryologie des Bothriocephalus latus." *Bull. Acad. impér. St. Petersb.*, t. xiv., p. 178, 1869.

Leuckart, "Die menschlichen Parasiten," 1 ed., Bd. i., p. 757, Bd. ii., p. 867, 1863.

Bertolus, "Sur le développement du Bothriocéphale de l'homme." *Comptes rendus*, t. lvii., p. 569, 1863.

Braun, "Zur Entwickelungeschichte des breiten Bandwurmes:" Würzburg, 1883.

Schauinsland, "Die embryonale Entwicklung der Bothriocephalen.' *Jenaische Zeitschr. f. Naturwiss.*, Bd. xix., 1885.

The problem of the occurrence and development of *Bothriocephalus latus* has only received satisfactory solution during the last few years. Since this tape-worm is found especially in districts where water is very abundant, and since the nearest relations of this worm are found mostly in aquatic animals, the opinion has been for long expressed that the intermediate host of this parasite was some aquatic animal, which transmitted it in its young stage to man. Fishes were first thought of, and it was sometimes supposed that the delicate trout and salmon were the hidden homes of the *Bothriocephalus* embryos.

The probability was increased, when Schubart of Utrecht, according to a communication of Kölliker's,[1] developed the ova of this tape-worm in water, and observed the liberated embryo with its mantle of cilia. Schubart's observations were unfortunately not published in detail.[2] They would perhaps have been forgotten, had not similar investigations, twelve years later, pursued contemporaneously in Russia, France, and Germany, by Knoch, Bertolus, and myself, led essentially to the same results. All agreed that the development of the embryo occupied usually several months, varying with external conditions, and especially with the temperature. The liberation only occurs during the warm season, so that ova formed in September are not liberated till April of the next year. Except in the ciliated envelope, which surrounds them at some distance, the embryos essentially resemble the long-known embryos of *Tæniæ*, especially in bearing the characteristic hook-apparatus.

[1] *Zeitschr. f. wiss. Zool.*, Bd. iii., p. 86, 1851.

[2] The reports which Verloren gave at the Assembly of Naturalists at Bonn (Tageblatt, p. 19, 1855) as to the observations of his deceased friend, do not really extend the communications of Kölliker except in expressly tracing the ciliated embryos to *Bothriocephalus latus.*

It was then established by Bertolus and myself that the ciliated embryos of *Bothriocephalus latus*, like those of other forms since discovered, serve just as do the similarly ciliated embryos of *Distomum* for enabling the free embryo to migrate into a temporary host, in which the further development to a cysticercoid intermediate form occurs. This, of course, suggested aquatic animals, having the same habitat as the free-swimming embryo. That fishes were thought the most likely subjects is not surprising, since these are not only the most frequent prey of all aquatic animals, but also because in the flesh and viscera of fishes Cestode larvæ had not unfrequently been found encapsuled, which, from the structure of their heads and other organs, might be young stages of *Bothriocephali*. In fact, Bertolus did not hesitate to claim as the intermediate form of *B. latus* one of these larvæ described by Rudolphi as *Ligula nodosa*, and parasitic in various Salmonidæ.

Fig. 374.—Free-swimming embryo of *Bothriocephalus latus*. (× 600.)

The reasons which Bertolus gave for his opinion were, indeed, scarcely sufficient to establish the connection of the two forms; and that the less since *Ligula nodosa* is a parasite of a very debateable character.[1] We were, however, led to attempt a solution of the problem experimentally. For this purpose, with the consent of the owner, I put a large quantity of ova and free-swimming embryos, enough to infect hundreds of fish, into a trout-stream[2] near my home, then in Giessen. The result was unfortunately negative, all the trout which I examined—in all more than two dozen—at various intervals up to two months after the introduction of the embryos, were free from the expected parasites. Similar experiments on certain species of *Cyprinus* also failed. The fact, which I then learned, that Bötticher had, in a *post mortem* examination of a woman who had died in poor circumstances at Dorpat, and who had for weeks before her death eaten neither fish nor flesh, found almost a hundred *Bothriocephali*, which, except one about a yard long, only measured a few inches, and must therefore

Fig. 375.—Encapsuled larva of a *Bothriocephalus* from the smelt. (× about 20.)

[1] Diesing regards it ("Revision der Cephalocotyleen, Abtheilung Paramecotyleen," *Sitzungsb. d. k. Wiener Acad.*, Bd. xlviii., p. 232) as a separate portion of *Triænophorus*.

[2] First German edition of this work, Bd. ii., p. 867.

have found their way thither not long before,[1] led me to think that not fishes, but perhaps smaller aquatic animals, such as Naiadæ, which harbour the related tape-worm *Archigetes*, might be the intermediate hosts of *Bothriocephalus*.

In opposition to Bertolus and myself, Knoch lays but little stress in the process of infection on the ciliated embryos. He attributes to them only the *rôle* of increasing the range of distribution, and facilitating the transmission of the embryo. From his feeding experiments, he concludes that this ciliated stage is not necessary in the life-history of the parasite. Infection is effected equally well, and indeed more frequently, by eggs, and it is indifferent whether these contain an embryo or not. It occurs, as in the *Tæniæ*, even when proglottides with ova are conveyed to the alimentary canal of the future host. There is no change of host, the transmission of the ova is directly followed by the development of the sexually mature form, so that man acquires the *Bothriocephalus*, not from fishes or lower animals, but directly from eggs or embryos which he has swallowed, usually in drinking water.

In support of these assertions, Knoch cites, as we have said, the results of the experiments made by him on dogs and other mammals. In seven different cases these were fed partly with ova, and the associated proglottides, partly with the ciliated embryos. Investigation of the victim, sometimes after several weeks, sometimes only after months had elapsed, gave in three cases (in a dog, a cat, and a rabbit) entirely negative results. In the other instances, which were all dogs, *Bothriocephali* were found in the gut, but only a few (at most seven, and in one experiment, made by Pelican, only one), and these at very different stages. Although the number of parasites contrasted strikingly with the hundreds and thousands of ova used for feeding, and although the degree of development did not seem to agree with the period which had elapsed, Knoch was so convinced of the cogency of his experiments, that he forthwith declared the result as requiring no further confirmation. And this opinion persisted even till a time when I had for long emphasised the insufficiency and the inadmissibility both of the proof and of the method of experiment, noting that the dog under ordinary circumstances can by no means be regarded as free from *Bothriocephali*, as was asserted by Knoch, but is, on the contrary, according to both older and more modern

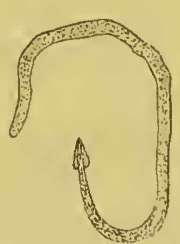

FIG. 376. — Young *Bothriocephalus* from the alimentary canal of the dog. Reared, according to Knoch, from immature ova. After Knoch (nat. size).

[1] *Sitzsb. Dorpater Ges. f. Naturw.*, Feb. 1871.

helminthologists (Linné, Pallas, and Krabbe) infected by them in all localities where the parasite abundantly occurs.

It is now unnecessary to criticise in detail[1] these statements maintained by Knoch with so much confidence, yet it is perhaps not superfluous to remember that the long period of incubation, and the character of the embryos, are facts which Knoch had opportunity enough to observe, and are of themselves enough to cast doubt upon his results, nor have I, though sufficiently convinced, omitted to repeat Knoch's experiments. In Giessen, where there are no *Bothriocephali*, I have not only experimented on dogs, both young and old, with fresh ova and with ciliated embryos, but have, along with several of my pupils (more than eight persons), swallowed each a dozen embryos, without ever obtaining anything but a negative result.[2]

Recent progress has thoroughly justified my opposition to Knoch, and it has meantime been experimentally proved by Braun that *Bothriocephalus latus has* an intermediate host, in which alone its development is perfected. This intermediate host is a fish, and especially the pike, an animal which, according to Braun's researches in Dorpat (long known as a home of *Bothriocephalus*), so frequently contains larval forms of this parasite, that among the specimens from the Peipus, the Wirzjaw, and the Eubach, it is very rarely that one is found without parasites. The worms are found encapsuled, not only in the most varied positions in the viscera, but also in the muscles, and usually in considerable numbers, so that pikes of little more than a span long sometimes contain in the flesh alone thirty or more.

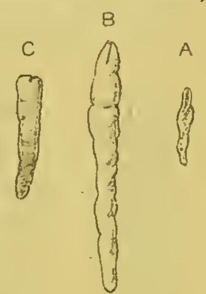

FIG. 377.—Larvæ of *Bothriocephalus latus* from the pike. *A* and *B* with extended, *C* with contracted head. (*A* nat. size, *B* and *C* × 3.)

The pike, though the favourite, is not the only host of this worm. It occurs also, according to Braun, in the burbot (*Lota vulgaris*), in the same organs as in the pike, but less constantly and less abundantly. It is possible, further, that in course of time we shall become acquainted with other fish which are intermediate hosts of this *Bothriocephalus*.[3]

[1] See also my remarks published at the time (*loc. cit.*), and also the criticism of Braun (*loc. cit.*, pp. 6-12).

[2] *Loc. cit.*, Th. i., p. 764 ; Th. ii., p. 867.

[3] Thus Dr. J. Ijima, Tokio, informs me that in Japan, where *Bothriocephalus* is frequent, the pike hardly ever occurs. He conjectures that the cystic form is harboured in the species of salmon (*Onchorhynchus Huberi* and *O. Perryi*), which are eaten not only salted and fried, but in certain districts raw in sauce, like bonettas, mackerel, plaice, carp, &c. Fish form an important constituent of food throughout Japan.

As found in the pike, the worm is long and narrow, not flat, however, but somewhat round and distended.[1] It varies in length from 1 to 2·5 cm., and in breadth from 2 to 3 mm. When much contracted, the body assumes, of course, a more compact form, the longitudinal diameter becoming reduced by more than half, and the thickness increasing in proportion. This is especially seen in front, where the head, as seems always the case in the pike, is invaginated, so that the subsequent external surface is wholly turned inwards, bounding a narrow irregular cavity, which begins with a distinct depression in the middle of the anterior end, and is about 0·5 mm. deep. If the parasites be put into luke-warm water, salt solution, albumen, or gastric juice, and kept at the temperature of an incubating apparatus, the head is usually evaginated. It appears as a more or less club-shaped or glandiform top, hardly 1 mm. in length, bearing on each of the sides which correspond to the greater transverse diameter of the body a rather shallow suctorial groove, thus agreeing essentially with the head of the future *Bothriocephalus.* Like the head end, so also the rounded thin posterior extremity is not unfrequently retracted, though only of course to the extent of a small inconspicuous depression. There is, as we should expect, *à priori*, no trace of a proper caudal bladder (see p. 377). The body throughout its whole extent is solid, and in structure essentially similar to the adult, but without reproductive organs, and without segmentation, although transverse wrinkles produce at first sight a similar impression. In comparison with the adult *Bothriocephalus*, the multitude of calcareous corpuscles is very striking; they are almost uniformly distributed through the body, and in such numbers that the larvæ when fresh appear almost white. In moist warmth the worm makes very energetic movements. Not only is the head repeatedly protruded and retracted, while one wave of contraction after another passes over the body, but the worm bends and straightens alternately like a whip, and the head presents many changes in form and general appearance.

Fig. 378. —Larva of *Bothriocephalus latus*, with protruded head. (× 6.)

The capsule round the worm is not at all firm, so that not unfrequently, especially on the intestinal wall, the worms are seen with one end projecting into the body-

[1] Through the kindness of Prof. Braun, I have been enabled to examine a large number of bladder-worms from the pike, and resulting *Bothriocephali* of different sizes, for which I feel constrained to express my gratitude here.

cavity, or quite free within the latter. Under favourable circumstances they may be kept alive as long as eight days outside their host.

Such were the forms which Braun experimentally demonstrated to be the young stages of *B. latus*. He experimented first with cats and dogs, in which the absence of *Bothriocephalus* was carefully proved beforehand by examination of the fæces and the administration of anthelminthics. The animals (seven cats and nine dogs) were each infected with a definite number of larvæ, which were mixed with the carefully inspected food. The examination of the host took place at various periods, after some days or some weeks. Only in two cases, in a cat and in a dog, was the result thoroughly negative. In a third case of a cat, which in consequence of repeated treatment with kamala and castor oil, was affected with enteritis, there was found in the thick intestinal mucus a single *Bothriocephalus*, little modified, but still living, though with the posterior end somewhat lacerated. In all the other cases, however, tape-worms were found, in numbers varying

Fig. 379.—Young *Bothriocephali* from the intestine of the cat, after feeding with bladder-worms from the pike (nat. size).

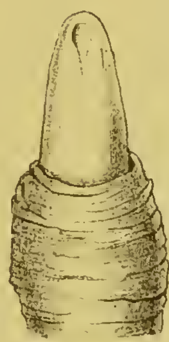

Fig. 380.—Head of a *Bothriocephalus* reared in the cat from bladder-worms from the pike, after Braun. (× 36.)

with the abundance of the feeding, and at degrees of development corresponding to the periods which had elapsed since infection. A dog which was still sucking, and which had been fed with seventeen bladder-worms, exhibited, ten days later, fifteen tape-worms, which, in spite of the absence of reproductive organs and their small size (from 9 to 14 cm. in length), were undeniably specimens of *B. latus*. In another case, in which the animal (a cat), after an interval of six or seven weeks, was again fed with flesh of the pike and burbot till the examination ten days afterwards, three *Bothriocephali* were found in the gut, half a metre long and six or seven weeks old, with at least 400 joints, of which the last exhibited almost mature reproductive organs and eggs within the uterus; but besides these were

found a large number of smaller worms at various stages of development (one to ten days old). The smallest differed from the *Bothriocephali* of the pike used for feeding, only in the constant evagination of the head, while the largest, measuring 15 cm. in length, already exhibited a distinct segmentation, though no reproductive organs were recognisable to the naked eye. The size of the others varied from 2 to 8 cm.

Not only in the dog and cat, however, but also in man, successful experiments led to positive results.

The experiments were made on three of Braun's students in Dorpat, who volunteered for the purpose. None of them had ever suffered from *Bothriocephalus*, nor did any one expel ova of *Bothriocephalus* at the commencement of the experiment. In the end of October, two of them (A and B) swallowed three, and one of them (C) four, freshly removed *Bothriocephalus* larvæ in milk, sausage, or bread, After the lapse of a month, 30 to 40 ova of *Bothriocephalus* were found in the first preparation made from the fæces of each, while eight days previously slight intestinal pains had been felt, which were due to the growing worm. The expulsion, which was brought about a few days after, resulted in the case of A in two *Bothriocephali*, in the case of C in three, and in the case of B in a number of fragments, which probably originated from several specimens. The average length of the worms was estimated at about 335 cm., the average number of joints at 1209, so that the growth of the worm day by day must, on an average, have resulted in a length of about 8·8 cm., representing thirty-one or thirty-two proglottides of average size. Since, however, the growth takes place at the anterior end, where the joints are mostly very small, the number produced daily must be much greater than Braun computes. Thus it is also explained how the worm, with increasing age, attains an ever greater length. During their four weeks' growth the worms had liberated no proglottides, as was also evident from the character of the terminal joint, which had an elongated tongue-like form, instead of the more or less degenerate semicircular form, which is exhibited in other cases as the result of a separation of the joints which does not anatomically coincide with the boundary of the segment.

In comparing this tape-worm reared in man with that from the cat, one is struck by the fact that the former has, in a shorter time, grown much larger, and formed far more joints than the latter. Nor is this true only of the general structure, but also of the individual parts. The head of the worm from the cat is markedly smaller, the anterior portion of the body extended and thin, the rest of the chain narrow and lean, and composed of joints which are for the most part much elongated. There cannot, however, be any doubt as to the rela-

tionship of the worms. The differences evidently result from differences in the hosts, and similar instances are found in the case of other parasites. The *Bothriocephali* found normally in the dog are also (according to Braun) far inferior to those of man, both in length and thickness. The head only measures a third of the usual size, the joints are smaller and flat, and in some cases thinner than in the above-mentioned *Bothriocephali* from the cat.

Satisfactory as are the conclusions to be drawn from such experiments, our knowledge as to the actual progress of development is still very incomplete.

Only the processes of formation of the embryo are really known, which have been recently elucidated by the work of Schauinsland above referred to.

We have already (p. 321) noted that the mature eggs of *Bothriocephalus latus* include within the ovum proper a large quantity of granular yolk-cells, and are surrounded by a hard shell with an operculum. The germinal vesicle, hidden amid the yolk mass, is rarely visible without special treatment, at least after the shell has become quite brown. When the eggs are laid they have generally already passed through the first stages of development. Under favourable circumstances, a clear spot can be seen through the shell amid the yolk spheres, which gradually increases to form the rudiment of the embryo. The yolk-cells, as is well known, take no direct share in the formation of the latter. They persist for a while unmodified, and then, breaking up, are absorbed as nutritive material by the cells of the embryo.

FIG. 381.—Ovum of *Bothriocephalus latus*, with yolk-cells and shell. (× 300.)

The first changes in the ovum have not been observed. From subsequent processes, however, they seem to consist in a segmentation which after the first cleavage into two becomes unequal, resulting in products which differ in position and appearance. The one set are the true embryonic cells. At first, four in number, they occupy as before the middle of the ovum, while the others, also few in number, become separated off, pass through the surrounding yolk-cells to the surface, and there form by flattening and peripheral coalescence a thin, clear, enveloping membrane, which persists for a time, and is sometimes recognisable, along with the remnants of the yolk, even till the liberation of the embryo. There can be little doubt that these enveloping cells represent the covering cells which have been already mentioned in connection with the cystic tape-worms, and which van Beneden[1] has since described in the development of the *Tæniæ* as

[1] *Archives de Biol.*, t. ii., p. 185, 1881.

"cellules albuminogènes." But the four embryonic cells lying inside the yolk are not all of the same nature. There is one among them which is seated as a cap upon the others, and which pursues a separate

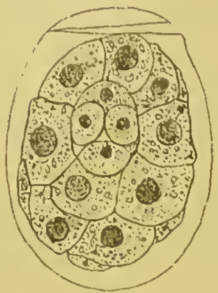

FIG. 382.—Ovum of *Bothriocephalus latus*, after Schauinsland, with four embryonic cells and enveloping cells on the granular yolk (× 600).

FIG. 383.—Another ovum, with covering cells apposed to the embryonic body. (× 600.)

course, inasmuch as, instead of dividing further along with the others and helping to form the embryo, it grows round them, and, along with its descendants, is gradually modified in the course of time into the ciliated mantle. As van Beneden has observed—and I can now confirm the statement—the chitinous shell surrounding the embryo of *Tænia* originates in exactly the same way. It is the result not of a simple secretion, but of a number of cells ("cellules chitinogènes"), which at an early stage separate from the rest and grow round them in the form of a pellucid membrane, which gradually thickens, and is modified into the subsequent shell. The ciliated membrane of the *Bothriocephali* is thus morphologically equivalent to the firm egg-shell of the cystic tape-worms and the associated egg-membrane, but not, as I formerly (p. 326) believed, to the peripheral border cells. There is, indeed, both anatomically and physiologically, a considerable difference between the two organs. From the originally thin and transparent envelope there arises no thick and firm chitinous shell, but a soft membrane, which, by the separation of the primarily closely apposed cell-walls, is divided, at a somewhat

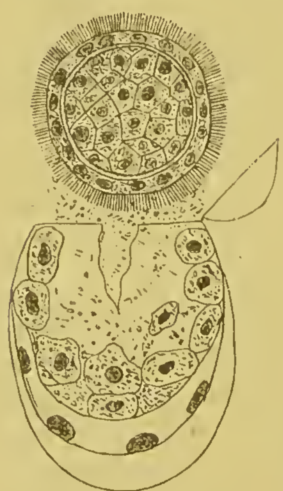

FIG. 384.—Egg of *Bothriocephalus*, with imperfectly developed embryo, being expelled by compression. In the interior of the egg-shell are seen the remains of the yolk-cells, and the enveloping membrane with its nuclei. (After Schauinsland.)

early stage, into two concentric lamellæ, between which lie a number of coarse-grained protoplasmic masses, with numerous, somewhat large nuclei, which owe their origin to the multiplication of the few originally present. Thus the ciliated mantle does not consist, as formerly supposed, of a simple membrane, but of a double one, as has since been independently discovered by Schauinsland and myself. Even at a very early stage may be detected short and delicate ciliated hairs on the external membrane, but these do not become very distinctly visible till after some time, when they have considerably increased in size.

But while the mantle has originated in the manner which we have thus shortly described, the nucleated mass of embryonal cells in its interior has been transformed by continuous enlargement and cell division into a clear solid body of round form, which is somewhat sharply defined, and which may be recognised as the true embryo by the rapid increase of the primary cilia. And this is still more evident from the fact that in the meantime the yolk-cells surrounding the mantle have, for the most part, entirely broken up, and, except numerous granules, have only left some larger or smaller irregular drops. One may occasionally still recognise some altered yolk-cells, with fluid contents, and with few granules.

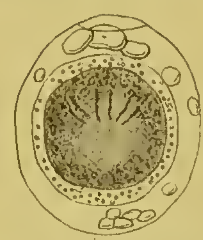

FIG. 385.—Embryo of *Bothriocephalus latus* in the egg.

When the development has progressed further, the previously visible motions of the embryo become more marked. The body

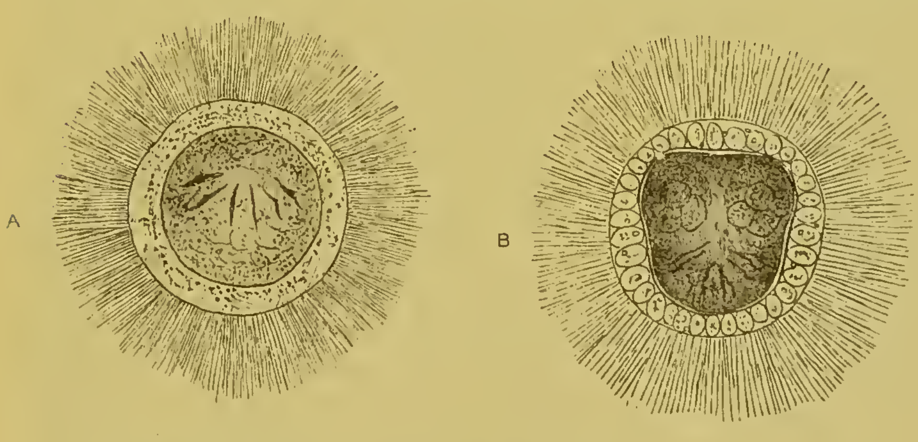

FIG. 386.—Free ciliated embryos of *Bothriocephalus latus.* (× 500.)

shortens and lengthens alternately, and the hooks are moved, until the lid opens and affords an exit. In slipping out, the body and its

mantle are squeezed through the narrow opening, and the play of the ciliated hairs begins, if it have not previously begun in the interior of the egg. The liberated embryo immediately resumes its round form, and swims about in the water by means of its cilia, rotating continually on its axis, with the hooks directed backwards. The cilia are extremely thin and delicate, and can only be recognised to their full extent in a good light. They are disposed very close to each other, and in contradistinction to the other species (Fig. 386), and also to Knoch's description, are of so considerable a length that they exceed the diameter of the embryonal body. In the interior of the egg-shell one usually sees, besides the remains of the yolk-cells, the nucleated enveloping membrane.

The period of incubation is extremely variable, being determined by the surrounding temperature and the depth of the water. In the middle of summer, when the eggs had been kept in flat saucers, I have often seen the embryos escape before the end of a month, and in the incubator, with a temperature of 37·5° C., after fourteen days. Under other circumstances, several months, or if the winter intervene, many months (eight or more), may elapse before the embryos are hatched, even when the extent of their development suggests that they should have come out some time previously.

In the free state the embryos continue to live and move for some days, sometimes more than a week. By means of their cilia they swim constantly, but somewhat slowly and heavily, through the water. The form of the body is but little altered, though sometimes rather elongated and sometimes shortened, so that the poles become flattened, or there may even be formed a slight pit or depression. This is especially true of the anterior hookless pole, which during strong contraction is broader than the posterior. After a short time the two lamellæ of the mantle separate considerably from each other owing to the inception of water. The mass enclosed between them becomes consequently clearer and more transparent, and the nuclei, formerly so numerous, disappear. In place of these, however, it now appears (Fig. 386, *B*) as though the space between the lamellæ were occupied by clear vesicular spaces, closely arranged in a single layer, so that they flatten out almost prismatically at the points of contact, and squeeze between them the granules which were originally more equally distributed throughout the whole mass. I have previously (p. 329) interpreted these vesicles without hesitation as cells, as Bertolus had also done, but now I find myself compelled to modify my opinion, and to regard them as vacuoles, which have probably arisen simply in consequence of the absorption of water. In this interpretation I differ on the whole but little from Schauinsland, who refers this appearance of

the embryos to the presence of protoplasmic threads, which extend in regular order between the two lamellæ, and thereby simulate cells. Just as the two lamellæ of the mantle are connected with one another by threads, so, too, do threads connect the embryo with the mantle, but the latter are considerably fewer in number and less strongly developed (Schauinsland). They are best seen in embryos which have lived for some length of time in the water, and in which the space below the mantle has been enlarged by the absorption of water. In the interior of the embryonic body, which has a diameter of 0·045 mm., and is thus considerably larger than that of the human bladder-worm, one recognises in successful preparations not merely the fibrous strands which are inserted on the roots of the hooks and move the latter, but also a tissue of very vesicular cells, which is surrounded on all sides by smaller cells, and occupies especially the hookless half. This does not consist, however, of a simple connected mass, but is divided into four adjacent balls by the fibres and cortical cells which insinuate themselves into it. The hooks themselves are strongly developed (0·015 mm. in length), and provided at the ends with a sharply defined sickle-like claw, 0·006 mm.

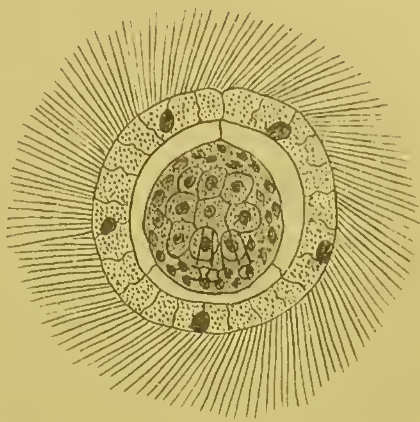

Fig. 387.—Free-swimming embryo of *Bothriocephalus latus* with the protoplasmic threads between the body and the ciliated mantle. (After Schauinsland.)

The longer the embryo lives freely, and the more the mantle becomes inflated, the more do the embedded granules disappear. In the same way, the activity of the cilia decreases and the motion becomes slower. At last the embryo sinks to the ground. The ciliary activity ceases, but the movements of the hooks and the contractions of the body may still be observed for some time. In many cases, however, the mantle has already been stripped off, so that the embryo is now completely free, and moves about with lively movements of the hooks and of the body. It not unfrequently happens that while the embryo is escaping, only the external lamella of the mantle is rent, and in

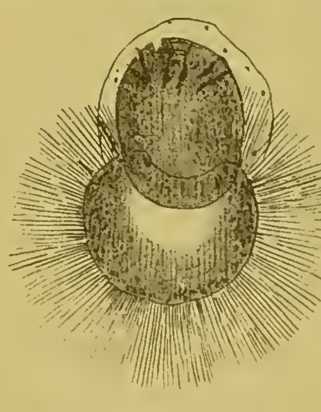

Fig. 388.—Embryo of *Bothriocephalus latus* escaping from its ciliated envelope.

such cases the inner one remains for a time in connection with the embryo in the form of a distinct delicate skin, presenting the appearance of a clear albuminous layer (Fig. 388). It is difficult to determine how long the worm can continue in this free condition without the mantle. Its appearance is for some time so thoroughly normal, and its mobility so great and constant, that I cannot agree with Knoch, who is inclined to regard the bursting of the mantle and the issue of the embryo as signs of a miscarriage. On the contrary, I should consider it probable that, as in the ciliated embryos of the Trematodes, this event takes place when the animals enter their intermediate host. If my opinion be correct, the ciliated coat is of use only in the search for the latter. For the embryos do not enter the tissue of their host from the intestine, but make their way directly into it from without, and in so doing they are much aided by the powerful movements of the hooks and of the whole body.

This process has unfortunately hitherto quite escaped observation. All attempts to bring about an immigration of the embryos of *Bothriocephalus* have failed. I have several times kept young pike for a week in the same aquarium with ciliated embryos without infection taking place. Just as unsuccessful were the experiments of Schauinsland, who several times, by means of a pipette, introduced a large number of ciliated embryos into the stomachs of young burbots, but could not find that they had bored into the walls of the intestine, or even pierced them. Twenty-four hours later they were found usually still living, and for the most part still surrounded by their cilia, chiefly among the pyloric cæca.[1]

These negative results are the more striking because it has been certainly demonstrated that pike and burbot are the intermediate hosts of *Bothriocephalus*. Whether the animals experimented upon were already too old for infection, or whether the embryos migrate, in the first place, into other aquatic animals, perhaps invertebrates, which are subsequently eaten by the fish when their inmates have attained a certain stage of development, are in the meantime open questions, which can only be answered by further investigations. The conditions of development in Trematodes, to which we have already referred, seem to favour the latter supposition; and that all the more since the larvæ of *Bothrioeephalus* in the pike and burbot were never observed by Braun in the first stages of development, and were always of a definite size (8 to 10 mm.). Braun, who inclines to the same opinion, advances a number of further observations in its favour. He finds that the larvæ are specially numerous in the wall of the intestine, and has observed

[1] *Loc. cit.*, p. 26.

some partly projecting out of it, and others free in the body-cavity, from which he concludes that it is possible that they reach the intestinal canal along with the first intermediate host, and that, after being liberated by the digestive process, bore through the intestinal wall and wander further.[1]

This being so, we are left to mere conjectures in regard to the changes which the six-hooked embryo undergoes in assuming its subsequent larval form. It seems probable, as we have already noted (p. 377), that the embryo, after migrating into its host, increases in size, loses its hooks, draws in one of the poles in order to form the head, and by continuous longitudinal extension grows into the subsequent larva. If the larval life of the worm be really divided between two intermediate hosts, these modifications will probably take place in the first, so that the second will only affect the parasite in so far as it affords the possibility of further growth.

If our views regarding the metamorphosis of the embryo of *Bothriocephalus* be correct, the larva which is formed from the latter represents a stage which we are quite justified in describing as "cystic." It is true that the bladder and head-rudiment exhibit very striking differences in form and structure when compared with those of others, say of the bladder-worm of the pig; but this need not at all affect our conclusion, since the nearest relatives of the true bladder-worms often present similar variations. We need only compare with these worms the above described *Piestocystis*, to see in their proper light the relations which exist between them. In both we find a solid, somewhat elongated, worm-like body, whose development from the six-hooked embryo can hardly be doubted, and in both

FIG. 389. — Young bladder-worm from the pike, with invaginated head. (× 6.)

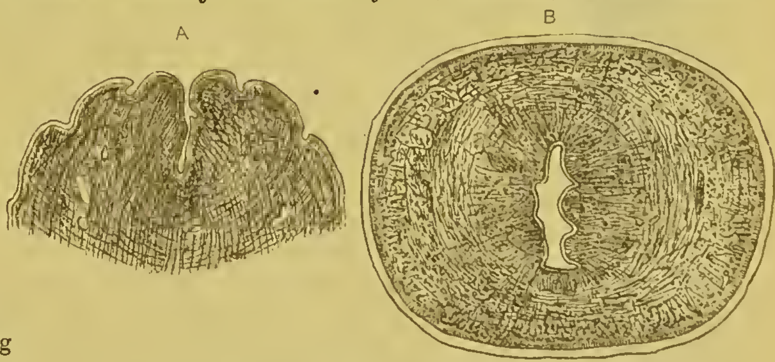

FIG. 390.—Head of bladder-worm from the pike. *A*, In longitudinal section; *B*, In cross section. (× 40.)

a retracted head without any sharp demarcation from the rest of the body. The fact that this head is still less individualised than in

[1] *Loc. cit.*, p. 50.

Piestocystis, is explained by the absence of the muscular suckers, which are so specifically characteristic of the head of *Tænia.* And the fact that in place of the four transversely placed suctorial grooves only two occur in *Bothriocephalus,* is also explicable; for it can be easily proved by means of sections that the invaginated head of the bladder-worm from the pike at first appears only as a flattened cavity, which is lined by a continuation of the cuticle, and which, extending in the direction of the shortest diameter (*i.e.* at right angles to the broad surface), sinks in for some distance from the anterior end of the body. Only after more minute observation does one perceive around the cavity (especially in transverse section) the parenchyma of the invaginated head with its muscular fibres, which form externally a sort of receptaculum, distinctly separating the head from the rest of the body. On the right and left, close to the receptaculum, one can now distinguish the lateral nerve cords.

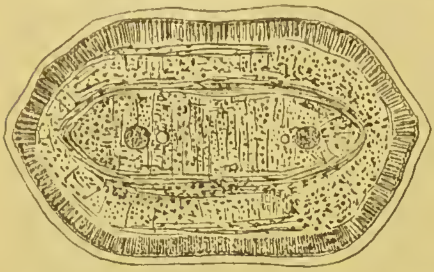

FIG. 391.—Transverse section through the body of a larva of *Bothriocephalus.*

How this larva changes into the jointed tapeworm after its transference to the final host has not yet been investigated. Braun's observations, which alone are available on this point, only show that, soon after entering the digestive apparatus of the final host, the larva stretches out the hitherto retracted head, and fastens itself by its aid to the intestinal wall; and that, after losing the calcareous corpuscles, which were previously very numerous, it grows with considerable rapidity, so that in a few days it may measure 6 cm. in size, and exhibit a somewhat indistinct segmentation. The increase in size affects not only the body, but also, and perhaps sooner, the head, whose form at the same time is more definite, and like that of the adult worm.

FIG. 392. — Sagittal longitudinal section through the protruded head of a bladder-worm from the pike. (× 40.) This section is taken to one side of the middle line, so that the lips of the suctorial pits limit the latter externally.

Whether the larval body is entirely or partially lost during this modification is uncertain. The description given by Braun almost leads us to infer the contrary, although in his observations no special attention seems to have been directed to the history of the larval body. The histological structure in no way contradicts such a supposition, for, as we have already seen (Fig. 391), the larval body in all essential points

resembles that of the adult form. It can at the most be said that its musculature is inferior in development and strength. But this is only true when the developed joints are included in the comparison, for the neck of the *Bothriocephalus*—and, as may be readily conceived, only this ought to be compared with the larval body—presents hardly any characteristics beyond those exhibited by the bladder-worm from the pike. Even the musculature of the head of the larva, when protruded, exhibits exactly the same relations as subsequently, and consists of direct prolongations of the longitudinal fibres of the body.

Distribution and Medicinal Significance.

While the large-jointed *Tæniæ* of man, and especially *T. saginata*, may almost be regarded as cosmopolitan parasites, the distribution of *Bothriocephalus latus* is much narrower, and its occurrence more restricted. It has hitherto been observed with certainty in but few places outside Europe. According to Verrill, it is found, though but rarely, in North America, and, according to Baelz and Ijima, it is frequent in Japan. In Europe, moreover, it only occurs in certain countries and districts. The most noteworthy localities are the coasts of the Baltic, especially the more easterly, and Switzerland, particularly the west. As is well known, the latter country furnished the first instance of *Bothriocephalus*. According to Zaeslein,[1] to whom we owe very thorough information regarding the occurrence of *Bothriocephalus* in Switzerland, the worm was formerly principally confined to the shores of the Lakes of Biel, Murten, Neuenburg, and Geneva. These localities may still be described as the principal seats of the parasite, although in some places—for example, in Geneva, where, according to Odier, a fourth of the population suffered from it—it has in the course of time become much less frequent. On the other hand, there are still places on the shores of these lakes (for example, Nidau, on the Lake of Biel) in which one adult out of every five suffers from this tape-worm. Children under ten are usually exempt. Some leagues (not more than four) from the water, *Bothriocephalus* is found much less frequently, especially among an agricultural population. The same is true in a greater degree of the more distant parts of the surrounding country, for there the worm appears only in the towns, usually in consequence of transference, and is only in a few places (Burgdorf and Thun) autochthonic. In the rest of Switzerland *Bothriocephalus* only occurs sporadically, although there may be no want of lakes abundant in fish. Huss[2] reports that among the sea-coast popu-

[1] *Correspondenzblatt für schweizer Aerzte*, Jahrg. xi., p. 673, 1881.
[2] "Ueber die endemischen Krankheiten Schwedens:" Bremen, 1854.

lation of the Swedish province of Nordbotten no one, whether rich or poor, old or young, is exempt,—not even unweaned children. Further inland in this case also the worm becomes gradually less frequent, and at the distance of some miles hardly an instance is found. We are also informed by Schauinsland that on the Kurische Nehrung hardly one of the fisher-folk is free from the worm. In St. Petersburg the number of the *Bothriocephalus* patients is estimated at 15 per cent., and at Dorpat Szydlowski[1] found the eggs of the parasite in 10 per cent. of the fæces examined.

It seems that the worm is also very widely distributed in the interior of Russia. We know of its occurrence in Poland, as well as in the southern provinces, where Pallas had already observed it, The dwellers on the shore of a lake near Kasan are said to be afflicted by it with special severity (Knoch). In Moscow, on the other hand, the parasite occurs but rarely. Of 200 tape-worm patients chronicled by Krabbe,[2] noted in Denmark, twenty were infected with *Bothriocephalus.* Most of them came from Zealand, in which island, and especially in Sorö, the worm is anything but rare. In France and Italy [3] *Bothriocephalus* is found principally in the regions near Switzerland. It was observed in Holland by van Doeveren, and in Belgium by Spiegel, but apparently [4] has not since been noted in either of these countries. The occurrence of *Bothriocephalus* in Germany is mainly limited to the coast regions of eastern Prussia and Pomerania, but some cases, which are to all appearance autochthonic, have been noted in Hamburg, Berlin, Mainz, and Munich. A very interesting communication on this subject is made by Bollinger,[5] according to whom *Bothriocephalus latus* has, during the last four or five years, been observed no fewer than eight times in Munich (among twenty-seven cases of tape-worm), and exclusively in persons who, for some time before the appearance of the parasite, had not left Munich, and who, in the majority of instances (in five), were known to have resided on the banks of Lake Starenberg. As no similar cases were observed at an earlier period,

1 "Beiträge zur Mikroskopie der Fæces," Inaugural-Dissert., Dorpat, 1879, p. 51.

2 "Om Forkomsten af Bändelorme hos Mennesket i Danmark," *Nord. med. Archiv*, Bd. xii., No. 23, 1880.

3 Of fifty-seven cases of tape-worm which E. Parona observed in Varese, thirteen were due to *Bothriocephalus*, twelve to *Tænia solium,* and twenty-six to *T. saginata* (*Giornale Real Accad. di med. di Torino*, Marzo 1882). Regarding the occurrence of *Bothriocephalus* in the north of Italy, see also Perroncito, "Parassiti dell'uomo et degli animali utili," 1882, p. 250.

4 My esteemed friend Ed. van Beneden has just written to me of a young girl in Verviers who voided a *Bothriocephalus*, although (with the exception of a day spent in Aix-la-Chapelle) she had never left the place of her birth.

5 *Deutsches Archiv f. klin. Med.*, Bd. xxxvi., p. 277, 1885.

it seems very probable that in eonsequcnee of the inereased eommeree on the shores of Lake Starenberg, the fish from whieh is earried as far as Munieh, there has arisen during the last deeade a new centre of infection of *Bothrioccphalus.* It is likely that the infeetion was carried to this distriet, whieh has reeently been mueh visited, either from Russia or Switzerland, and that now it is itself a breeding-place of the parasite.[1] It is uneertain whether the sporadie eases which have been noted in London, St. Malo, Montpellier, Rome, and other places on thc Continent, are imported or autoehthonic.

Aeeording to the experiments of Braun, to whieh we have already referred, it ean no longer be doubted that the *Bothriocephalus* is introduced into man by eating fish, and particularly pike. It is true that the danger of infection is not everywhere equally great. As may be readily undcrstood, its degree is determined by the oecurrence and frequency, not only of the fish, but of the host, which in its turn infeets the fish. The infection may also be furthered in a very high degree by eertain loeal arrangements, and particularly by those whieh afford to the fæcal masses an unhindered and speedy entrance into the water, so that, as we have already seen, regular breeding-plaees of the parasite arise, from which, in proportion to the means of eommunication, it will be carried further and further by the intermediate hosts. If the fish be properly prepared and sufficiently boiled or fried, it may, of course, be eaten without injurious eonsequences, even if it contain larvæ of *Bothriocephalus.* But it is otherwise if the culinary proeess be not suffieient to kill the latter. Smoked pike, which in some plaees—*e.g.*, in Dorpat and its surroundings—forms a common artiele of food, is according to Braun especially dangerous, being often so earelessly prepared that he has several times found in the fish living larvæ. The degree of temperature required to kill them has not been thermometrically determined, but the faet that the worms remain alive even in hard frozen pike suggests a great power of resistance. We have already seen that only the pike and burbot have been proved to transfer the *Bothriocephalus.* This, however, by no means excludes the possibility that other speeies, perhaps even some of the most favourite edible fish, may yet be proved equally dangerous (see p. 717).

The oftener such fish are eaten, the greater is the danger of infeetion, and especially if little care be expended in eooking. Thus we find, for example, in Dorpat, that the poorer elasses, who live mainly on the previously mentioned smoked pike, are thc ehief sufferers from

[1] Huber has recently reported an instance of the occurrence of *Bothrioccphalus* in a coachman who had never left Swabia and Lower Bavaria (*Aerztliches Intelligenzblatt*, No. 8, 1885).

Bothriocephalus, and that, as Schauinsland has reported, not one of the fisher-folk in the Kurische Nehrung is exempt. In such cases it is also not at all uncommon for several members of the same family to be infected with the worm at the same time, or for several specimens to live together in the same intestine, as is, for example, expressly stated by Huss to be the case among the coast population of Nordbotten. We have already seen (p. 720) that the students to whom Braun administered several larvæ of *Bothriocephalus* produced almost the same relative number of young worms; and C. Vogt relates of himself that, after having lived eighteen months in the neighbourhood of Geneva, he once voided[1] eight of these worms at one time. Mention has already been made of Bötticher's case (p. 715), in which over a hundred young *Bothriocephali* were found. We may also consider it due to the mode of life that children, on the whole, but rarely suffer from *Bothriocephalus,* and that women, who are busied in the kitchen, are more liable than men. Of the eight tape-worm patients observed by Bollinger in Munich, only three were males, and among his twenty cases Krabbe only mentions one. In Varese, on the other hand, Parona found among thirteen patients only five women.

Our increased knowledge of the habits of intestinal worms has dissipated an idea which has been several times expressed, namely, that *Bothriocephalus* and *Tænia* mutually exclude each other. Cases of such a simultaneous parasitism are not wanting in recent literature, although the necessary conditions do not perhaps frequently occur.

It has, however, been proved by the above-mentioned feeding experiments of Braun that man is not the only host of *Bothriocephalus latus.* The occurrence of the worm in the dog has already been noted by Linné and Pallas, and more recent investigations in very various localities have confirmed these statements (von Siebold, Krabbe, Perroncito, and Braun). Whether the cat is infected spontaneously is less certain. It is true that Creplin found some specimens of *Bothriocephalus* in a domestic cat in Greifswald, but they were too young to be certainly determined.[2] So, too, the *Bothriocephali* which Krabbe observed in Copenhagen in a cat, and which he describes as 15 to 20 cm. in length, with large lancet-shaped head, and numerous calcareous corpuscles in the joints, are certainly different from *B. latus.*[3] Further, the *Bothriocephali* of the dog are by no means all of the same kind; for in Iceland alone Krabbe noted no fewer than three different species,[4] and probably the *B. cordatus* of Greenland ought to be regarded as a fourth.

[1] "Die Herkunft der Eingeweidewürmer des Menschen," p. 16, 1878.
[2] "Observationes de Entozois;" Gryphiswaldiæ, 1825, p. 67.
[3] "Recherches helminthologiques en Denmark et en Islande:" Copenhagen, 1860, p. 19.
[4] *Ibid.*, p. 27.

We must, however, remember that the specimens of *Bothriocephalus latus* occurring in the dog and cat not only develop much more slowly than in man, but differ more or less strikingly in size. It is true that the worms in man have not always the same appearance. This is sufficiently evident from the fact that, besides the real and typical *Bothriocephalus latus*, or in place of the latter, both the earlier and more recent Helminthologists have thought themselves justified in distinguishing several different species. Thus Linné spoke of *Tænia vulgaris* and of *T. lata;* Pallas of *T. grisea, T. lata*, and *T. tenella;* Göze of *T. membranacea* and *T. lata*—all of which, although regarded as *Tæniæ*, belong to *Bothriocephalus latus.*

These species were distinguished, not only on account of the false ideas which then prevailed regarding the structure of the head in *Tænia lata*, but especially on account of the different physiognomy of the worms, and the structure of their joints and uteri. Although Grassi [1] has lately tried to identify with Linné's *Tænia lata* the *Bothriocephalus cordatus* discovered by me, which we shall afterwards more specially consider, I must continue to regard it as a distinct species. On the other hand, I think that, notwithstanding its inconsiderable length (1·8 metre), and the smallness of its joints, the form described by the latter (without name), and also the *Bothriocephalus cristatus* of Davaine, ought to be regarded as belonging to *B. latus.*

The differences which can be observed in the worm are to be referred partly to an unequal state of contraction, and partly and more especially to differences in age, growth, and food. As Bötticher has already noted, there are "well-fed" worms, and others which are extremely emaciated and appear as thin as paper. The former are more or less coloured, yellowish or yellowish-brown, according to the distention of the yolk-glands, while the latter are colourless, and have but slightly developed sexual organs with few eggs. In the same way there are large and small *Bothriocephali;* some, with a size of 2 metres or even less, attain their full development, as is evident from the fact that in them the greatest breadth and greatest distention of the uterus do not coincide with the end of the chain, but usually occur some distance anterior to this, at least if a number of proglottides have not previously been cast off. Moreover, such examples are not only shorter than the average, but their joints are smaller, having a length of 2 to 2·5 mm., and a breadth of perhaps 5 to 6 mm., while usually the latter is double this, or even more (as much as 20 mm.). Thus it happens that the relations of length and breadth in the joints often vary throughout considerable portions, or even throughout the whole of the body; and under some circumstances the length of the joints becomes

[1] "Intorno ad un Bothriocephalus dell' uomo," *Ann. univ. di Med.*, vol. ccli., p. 8.

even greater than the breadth, so that this feature, formerly so characteristic of *Bothriocephalus*, disappears more or less completely. And this is all the more apt to take place from the fact that in such cases the uterus is usually considerably distended, and exhibits loops far separated from one another; so that, in place of the usual rosette-like form, a structure arises which is at first sight almost Tænioid in character. But in spite of their different appearance, these worms do not really differ from the typical *Bothriocephalus*. One has only, as Bötticher has shown, to treat them with warm water in order to see the joints greatly shorten, with simultaneous increase in breadth, until they finally assume the usual form of *Bothriocephalus latus*.

Not only the joints, however, but also the neck and head, assume, according to circumstances, a different form. The former is at one time slender and stretched out, so that the segmentation only begins at a distance of 15-25 mm. behind the head, where the breadth amounts to perhaps 0·25 mm. (Fig. 357), and at another time (Fig. 358) very broad and thick (1·5-2 mm.), and so short that the segmentation can be traced almost up to the head. The appearance of the latter is just as variable. During life, and even under the eye of the observer, it often changes its oval form (Fig. 358) for one more like a club. Further, the anterior end appears at one time flattened out, at another more pointed; the border of the suctorial grooves is sometimes straight and sometimes undulating, while the grooves themselves may be either narrow and contracted or wide open. All these states may be occasionally observed in preserved specimens.

A B

FIG. 393.—Club-shaped head of *Bothriocephalus latus*. *A*, Seen from the edge; *B*, From the flat surface. (× 8.)

In our description we have already shown to what considerable size *Bothriocephalus* may grow. Nor is even the length there mentioned the maximum which the worm may attain. Pallas mentions a specimen 56 feet long, and from other quarters also we have heard of unusually long specimens. If we consider that the worm does not, like the large-jointed *Tæniæ*, throw off the proglottides singly, but in portions several feet in length, and at irregular and often long intervals, and if, on the basis of the vegetative conditions established by Braun (8·8 cm. per day), we estimate the yearly growth approximately at 100 feet, it will be seen that the existence of such gigantic worms is by no means an impossibility.

This estimate of the growth almost entirely agrees with the statement of Eschricht regarding a patient suffering from *Bothriocephalus*, who within a year voided 70 feet of tape-worm, 20 of which, it is true, belonged to the parasite itself, which finally found an exit along with

its head. The amount cast off in the year, in pieces usually 2 to 4 feet long, may accordingly be estimated at about 60 feet. If the worm were expelled almost as far as the head, six to eight weeks would sometimes suffice to allow it to grow to 6 to 8 yards. At all events, the growth of *Bothriocephalus* is much quicker and more energetic than in the case of the large-jointed *Tœniæ* of man.

It is probably, too, on account of the unusual length of the worm and the great flexibility of its body, that it is by no means so easy to expel as one would imagine from the weak development of the attaching apparatus.

It is hardly possible to state with certainty how long the parasite may remain in man. It is probably not behind the large-jointed *Tœniæ* in this respect. At all events its existence may extend over many years. Bremser mentions the case of a native of Switzerland, who had lived for twelve years out of his native country, but had observed the presence of the worm only a year before, and as the stretches of joints contained in the fæces may easily escape notice, it is by no means impossible that the parasitism had extended over an even longer period. Mosler also reports two cases of *Bothriocephalus*, one of which was six years old, and the other probably fourteen, but certainly ten.[1] Since the ova, as we have seen, are allowed to escape in such great numbers that the uteri in the last joints, if these have remained for some time in connection with the rest of the chain, are usually quite empty, the examination of the fæces demonstrates the presence of the parasite with absolute certainty, even when it has been otherwise unobserved by the host. As a rule, however, the parasite soon makes its presence felt—according to Braun's experiment, three weeks after inspection—by occasioning difficulties in digestion, like those caused by the larger *Tœniæ*. These effects (gripes, loss of appetite, sickness, &c.) apparently follow the presence of *Bothriocephalus* with more certainty and intensity than that of *Tœniæ*, sometimes, or even frequently, producing nervous disorders, especially in women. Prolonged persistence occasionally produces marked emaciation, while other cases occur in which the worm does not cause the slightest inconvenience. The possibility of self-infection is seen, of course, to be excluded by the life-history of the parasite.

? Bothriocephalus cristatus, Davaine.

Davaine, "Traité des Entozoaires," second edition, supplement, p. 928 : Paris, 1877.

Some years ago Davaine described under the above title a form of *Bothriocephalus* which he regards as representative of a distinct species,

[1] *Virchow's Archiv f. path. Anat.*, Bd. lvii.

though its peculiarities do not appear to me sufficient to justify his opinion. His description was based on two specimens—one without a head, which was found in a man forty years old, from the Department of Haute Saône, while the other with the head was obtained from a child five years old in Paris.[1] The former measured 92 cm. in length, but was apparently much contracted, as might be inferred, not only from the segmentation, which extended close up to the head, but also from the form of the proglottides, which possessed considerable thickness, but were never more than 1·5 mm. in length, and had their posterior borders much protruded, so as to embrace in an almost cuff-like fashion the succeeding joints. At a distance of about 20 cm. from the head, the breadth of the chain increases abruptly from about 1 to 4 mm., and then gradually to 9 mm. The head, which suggested the name "*cristatus*," is said to be especially characteristic of this form. It is of considerable size (3 mm. long, 1 mm. broad, 0·6 mm. thick), and in shape resembles a grain of linseed with the point turned forwards. There are no proper suctorial grooves, but according to the description, the two surfaces of the head are each provided with a projecting ridge, which extends from the anterior apex, and is divided by a furrow into two longitudinal lips. These lips diverge posteriorly, and enclose a groove resembling the calamus scriptorius in the brain. The margins of the ridges are covered with small papillæ, and the rest of the head is marked by transverse wrinkles. Characteristic of this form are the numerous calcareous bodies, which penetrate the parenchyma of the head in four longitudinal strands, and extend in such abundance through the neck into the body that Davaine refers its thickness and stiffness to these deposits. The total length is said not to be more than 3 metres. The ova resemble those of *Bothriocephalus latus*.

Bothriocephalus cordatus, Leuckart.

Leuckart, "Die menschlichen Parasiten," first edition, Bd. i., p. 437 *et seq.*, 1863.

In the structure of its joints, this form is not unlike Bothriocephalus latus, *but on closer inspection cannot be confused with it, not only because of its considerably smaller size and more compressed form, but especially on account of the structure of the head and anterior end of the body. Unlike the extended, oval, or club-shaped head of* Bothriocephalus latus, *the head of this form is short, broad, and cordiform, with lateral borders, which*

[1] Davaine supposes, it is true, that his *B. cristatus* is of much more frequent occurrence. He refers to a report of Cobbold, according to which several worms preserved in the Westminster Hospital Medical School belong to his species, and also to an anonymous Memoir published in 1776 in Kempten, in which his worm is said to be figured in a thoroughly satisfactory fashion.

usually project from the surface, and are drawn out longitudinally on either side, into a deep and sharply defined suctorial groove. Behind this head extends, not a long, narrow, neck-like anterior portion, but the broad body with its segments, which are from the first readily recognisable by the naked eye, and which increase in size so quickly that the worm acquires anteriorly a lancet-like form. At a distance of 3 *cm. behind the head, the joints are already sexually mature, and* 3 *cm. farther back they have attained almost their maximum breadth* (7 *to* 8 *mm.). The number of immature joints is at the most about* 50, *and the great majority of these exhibit distinct genital apertures. Their immaturity consists only in the absence of hard-shelled ova. There is no distinction between median and lateral regions in the immature joints. These only become distinguishable with increasing maturity, when the median have a clear appearance, while the lateral portions are a dark grey colour, which gradually becomes more and more marked. The length of the mature joints is on an average between* 3 *and* 4 *mm., but the contractility of the worm is so great that they sometimes measure only* 1·3 *mm., with a corresponding increase in breadth and thickness. Only the terminal joints are exceptional, in having generally a square form,*

Fig. 395.

Fig. 394.

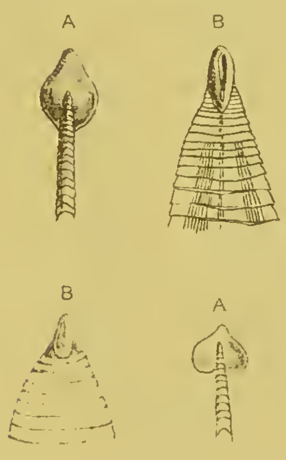

Fig. 396.

Fig. 394.—Head and anterior portion of *Bothriocephalus cordatus*, seen (*A*) from the side, and (*B*) from the surface. (× 5.)
Fig. 395.—A number of mature joints of *B. cordatus* (nat. size).
Fig. 396.—Uterus of *B. cordatus* (nat. size).

measuring each way 5 *to* 6 *mm. In the largest worms,* 115 *cm. long (with a head* 2 *mm. long and broad), there are about* 600 *joints, but the*

number is as a rule less, and usually only 400. *The middle of the dorsal surface is traversed by a longitudinal furrow. A similar longitudinal furrow is recognisable on the ventral surface below the genital apertures. Especially characteristic and distinctive are the form of the head, the great number of calcareous corpuscles embedded in the parenchyma of the body, and the structure of the uterus, which is not only narrower and longer, but exhibits a larger number* (6 *to* 8) *of lateral horns.*

This worm occurs in the north of Greenland (Godhavn), but has only been found once as yet in man. It is, however, frequent and abundant in the dog, and occurs also, according to Krabbe,[1] in the seal (*Phoca barbata*) and the walrus.

I owe my opportunity of investigating this new species to the kindness of my renowned friend Professor Steenstrup, who obtained the worm, along with a large number of other Helminths, from Dr. Olrik, the Danish Government Inspector of Northern Greenland. I was able to compare about twenty specimens, young and old, of which, however, only one was, as above mentioned, derived from the human subject. The latter was accompanied by a history of the patient, which, as translated from Professor Steenstrup, runs as follows:—"The worm was obtained from a half-breed, Koren Margrethe, married to a half-breed, Peter Broberg, in Godhavn (North Greenland, 70° N. lat.). The patient is thirty-four years of age, was married in her tenth year, and has four children. She expects in September next (1860) her fifth accouchment. Since the beginning of pregnancy, she has suffered from severe stomachic pains, associated with violent vomiting, and has been otherwise unwell, although in her former pregnancies she had not the slightest symptom of this kind. She was not able to eat anything young, neither young bird nor young seal. In the vomit there was no trace of tape-worm, but on the 30th June she voided with the fæces a long, broad tape-worm, which was unfortunately not preserved. Some days later vomiting again set in, and shortly afterwards (8th July) she voided a tape-worm (Fig. 397). This was smaller than the former, though it measured, when living, fully a finger-breadth in diameter. The patient had never before remarked anything of the kind, and had not even suffered from the Ascarides (*Oxyuris*), so common among Greenlanders. After voiding the worm, the patient (who it may be mentioned was the sister of my maid-servant) felt somewhat relieved. As the stomachic pains, however, did not cease, she presumed the presence of other worms. The vomiting, however, was alleviated. With the stomachic pains a watery diarrhœa was always associated, in the course of which both worms escaped. Before

[1] "Rech. helminthol.," p. 33: Copenhagen, 1866.

I left Greenland the excrement had become firmer, but the patient was still very thin, which was contrary to her usual tendency."

Whether the above history describes the symptoms of a helminthiasis, or the attendant effects of pregnancy, can, in spite of the

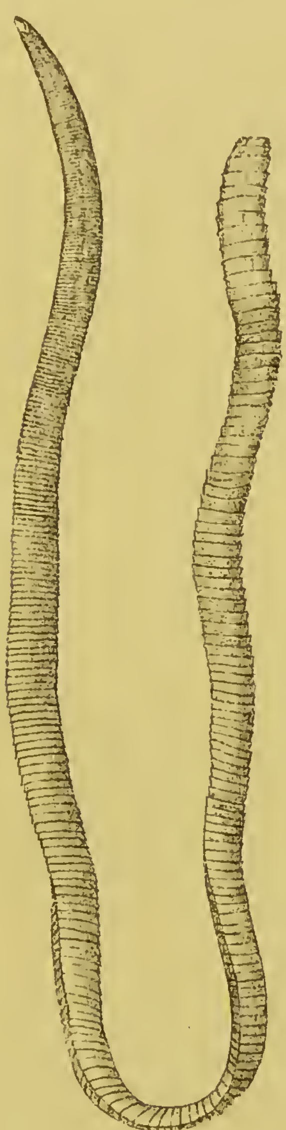

FIG. 397.—*Bothriocephalus cordatus* from man (nat. size).

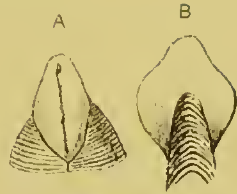

FIG. 399.—Three joints, seen (*A*) from dorsal, and (*B*) from the ventral surface. (× 2.)

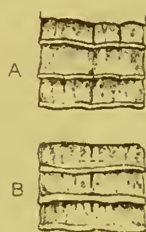

FIG. 398.—Head of the same (*A*) from the side, (*B*) from above. (× 8.)

antecedents, hardly be determined; the account serves, however, as documentary evidence of the occurrence of the worm, and is therefore included in the present account.

At first sight the worm appeared not a little different from the tape-worms of the dog which were sent along with it, though the

difference did not amount to the absence of any important character. The structure of the head and of the anterior part of the body, the disposition of the uterus, the abundance of calcareous corpuscles, left no doubt at all as to its identity; but the general habit was very different, so that a specific distinction was almost suggested. The total length was only about 26 cm., though the number of joints amounted to fully 300. The anterior hundred occupied about 30 mm., the middle hundred 100 mm., and the posterior hundred 130 mm. With a breadth of 6 mm., the individual joints were never more than 1·3 mm. long, and in a portion near the middle of the worm not more than 0·8 mm. Twenty millimetres behind the head, which measured about 1·5 mm. in both directions, the body had almost attained its full breadth (5 mm.).

The worm was characterised not only by the shortness of the joints, but by their thickness, which measured between 3 and 4 mm., showing beyond doubt that it was in a very contracted state. This resulted probably from the fact that the worm, immediately after being voided, and still in possession of its full muscular power, was thrown into strong alcohol. There were among the tape-worms from the dog other specimens, which were, in part or altogether, as strongly, or even more strongly, contracted. This was especially well seen in a worm, which, in spite of its 460 joints, measured only 164 mm. in length, and bore posteriorly proglottides only 1·3 mm. long. The breadth (7·5) was greater, of course, than in the above specimen, but the thickness, especially of the lateral regions, was much less.

Under the circumstances, I have not the slightest doubt that all these worms belong to the same species, and hence it seems to me certain not only that the Greenland dog harbours a species of *Bothriocephalus* different from *B. latus,* but also that this form occasionally occurs in man.

Further observations are indeed required as to the frequency of its occurrence in man. In the Greenland dog the species must be one of the commonest intestinal parasites, for all the specimens (about twenty) which I examined were obtained within half a year, and, with the exception of one, in three months; and that, too, at one place, Godhavn, the seat of the Danish Government inspector. The worms were derived from five dogs, of which two produced one each, a third two, a fourth eight, and the fifth all the others. These last were taken from the intestine of the dog after death, one of them still firmly attached to one of the villi; the others, some of which had lost the head, were spontaneously expelled from their hosts.

Whether this species occurs in other localities is still unknown. The report of its discovery in Dorpat has proved to be erroneous.

Grassi thought, indeed, that Linné's *Tænia lata* might be referred[1] to our *Bothriocephalus cordatus*, but from the description and figures[2] it seems to me as though it differed only in its greater contraction from the more elongated *T. vulgaris*, and thus simply represented a much contracted specimen of *T. lata*. Of *T. lata* it is indeed said—"rarissime in hominibus vermis observatur, vulgatissimus autem in canibus;" while in regard to *T. vulgaris* nothing is said of its occurrence in the dog, but merely, "vulgatissimus (vermis) inter Tænias homines infestantes;" but this alone is not enough, and the differences between the species as noted by Linné may perhaps be due to the worms from the dog having been examined in a lively and contractile state, while those from man were observed only when exhausted or even dead. The descriptions indeed suggest this supposition.[3] This much, at any rate, is certain, that the description of *T. lata* affords no decisive proof of its identity with our *B. cordatus*. The head, which ought to form the primary object of investigation, is not described either in *T. lata* or *T. vulgaris*, and was perhaps not even seen.

Be that as it may, a denial of the specific distinctiveness of *B. cordatus* seems to me henceforth impossible. Even the separated joints can be readily distinguished from those of *B. latus*, less perhaps on account of their form, though that, too, is diagnostic, than on account of the calcareous corpuscles, which are as abundant in the Greenland species as they are rare in the Swiss or Russian tape-worm. They are thickly distributed through all the layers of the body, and sometimes attain a size of 0·028 to 0·03 mm. The peculiarity in the structure of the uterus has been already noted. Similarly the stronger development of the muscles, especially of the longitudinal muscles in the cortical layer, must be noted as characteristic of *B. cordatus*, and this explains the striking contractility of the worm, as also the large size of the cirrhus-pouch (0·6 mm. long by 0·43 mm. broad), as compared with that of *B. latus*. These are, however, points of detail, and, for diagnostic purposes, unimportant in comparison with the structure of the head and anterior portion of the body.

In the larger worms the head has a length of 2 mm., and a proportionately large breadth. Viewed from the flat side, the anterior half appears pointed, while the lateral portions project posteriorly, more or less like wings, according to the degree of contraction

[1] *Ann. univ. di Med.*, vol. ccli., 1880.

[2] "Amœnit. Acad.," vol. ii., p. 71, Fig. 3.

[3] Thus it is said of *T. lata*, "Dum adhuc vivus est et se extendit, uno alterove loco filiformis evadit, et articuli iis in locis graciles fiunt, atque post ejus mortem lati sunt," while no mention at all is made of the living state of *T. vulgaris*.

exhibited by the head (Fig. 394). The shape of the head of course varies, but may be generally compared to the heart in a pack of cards, or to an arrow-head. The flattening increases gradually towards the point, but is, on the whole, not conspicuous, and least so in the posterior half, where the rudiment of the subsequent lateral margins of the body is recognisable.

The anterior half is distinguished, not only by its flattening, but also by the depth of its marginal grooves, which is so considerable, that they are separated from one another only by a thin partition. On the other side of the middle of the head, the depth and width of the grooves gradually decreases, until a shallow furrow alone remains. With the depth of the grooves the more or less free development of the limiting lips is associated. That the latter, even where most independent, are without any proper musculature, has been already mentioned as characteristic of the genus *Bothriocephalus*. The fact is readily demonstrated in transverse sections, in which one can also convince one's self of the general structural and histological resemblance between the head and the rest of the body. In the head, as elsewhere, a median layer and a peripheral muscular sheath are distinguishable, both but slightly diverging from the ordinary type. The internal wall of the marginal grooves is, of course, formed from the cortical layer, which is here so thick that the middle layer in the anterior half of the head is entirely displaced by the layer connecting the two lateral surfaces. In the middle layer, besides numerous calcareous corpuscles, the two nerve strands can be recognised, disposed opposite to one another in the direction of the smaller diameter.

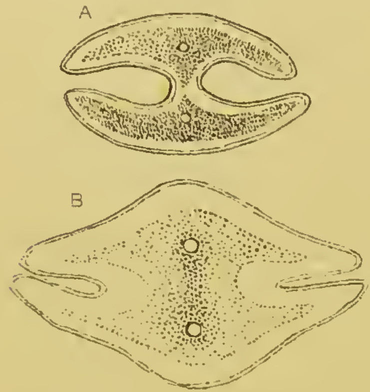

Fig. 400.—Transverse sections of the head of *Bothriocephalus cordatus*; *A*, before, *B*, behind the middle. (× about 20.)

The structure of the generative organs does not differ typically from that of *B. latus*; and I have not been able to elucidate their development. The ova closely resemble those of the Swiss tape-worm, but are on an average somewhat larger (0·075 to 0·08 mm. long, by 0·05 mm. broad).

It was to be expected from the analogy with *B. latus*, that *B. cordatus* would liberate its joints in groups, and not singly. The specimen (Fig. 397) obtained from the patient, as above described, most clearly suggested the occurrence of this process. At a distance

of 23 mm. from the posterior end of the body, an annular constriction was evident, 1·5 mm. deep at one lateral margin, and 1 mm. at the other, and separating off the last seventeen joints. A second constriction occurred 17 mm. further up, isolating an almost equal number of joints (fifteen), but less deep than the one behind.

I do not think I am wrong in regarding these grooves as the first signs of the commencing separation, and am confirmed in this opinion by the fact that they do not coincide with the boundaries of two joints, but extend across the surface of a joint. Since the end of the chain exhibited only half a joint with a cirrhus-pouch, my supposition seems fully justified.

Among the specimens of *Bothriocephalus cordatus*, there were, besides adult chains of joints, several young worms, which were of special interest on account of several peculiarities, which have not, so far as I know, been elsewhere observed in young *Bothriocephali*. It was even possible to form a tolerably complete series of such forms, and thus to elucidate in an unexpected manner the early stages of the species.

FIG. 401.—Four young specimens of *Bothriocephalus cordatus* (nat. size).

The smallest of these young worms measured not more than 30 mm. It exhibited, like the others, a clear, almost transparent appearance, due not only to the absence of cortical granules, but especially to the thinness of the body and the slight development of the muscles. The greatest breadth (3 mm.) was exhibited a short distance behind the head. The anterior end already showed the characteristics noted in the adult. The posterior third of the body was, however, strikingly different, becoming gradually narrower, and ending in a thin point. The head exhibited the adult form, but was of much smaller size (0·8 mm.), while the body was divided into about 140 narrow segments, of which those about the middle were not only the broadest, but also the longest.

The other worms exhibited a similar structure, and measured from 40 to 100 mm., increasing gradually in breadth to 5·5 mm. Not only did these larger specimens resemble the smaller in form, but even in the number of segments, which

varied from 125 to 154. The only differences associated with the growth of the joints and head (measuring over a millimetre) lay in the beginning of sexual development. Even in those 80 mm. in length I could recognise in the larger middle joints a generative aperture and cirrhus-pouch, and in the interior, in soaked specimens, the rudiments of the ducts, while in specimens 100 mm. long the generative apparatus could be seen in greater completeness and distinctness. The median region had at the same time swollen out into a longitudinal elevation, as in adult forms, evidently an indication of further sexual development. Curiously enough, it was the median segments of the body which were best developed, not only in size (1·2 mm. long), but in the structure of the generative organs; only in larger forms did this distinction disappear. In a specimen 27 cm. in length, with 184 proglottides, which had already liberated some of its posterior proglottides, all the joints except the anterior 40 to 60 were quite mature.

I thought at first that the above peculiarity was confined to this species of *Bothriocephalus*. Since then, however, we have learned, from the researches of Kahane[1] and Riehm[2], that in *Tæniæ* also the last joints of the chain are very often sterile and small, and that the sexual development always begins at some distance from the oldest joint. The number of these barren joints varies very considerably; though generally but few, they include in some species about half of the whole chain, and thus give the young worms a form strikingly different from that of the adults. In the case of *Tænia perfoliata* from the horse, the young form has, as Kahane has shown, been even regarded as a distinct species (*T. plicata*). The case of *B. cordatus* is probably similar; the last joints of the young chain probably remain sterile, and separate without further growth or development. *B. latus* seems, according to Braun's report, to be different in this respect, so that the present species probably exhibits also this difference in development, though it can hardly be supposed that it stands alone in this respect. In fact *B. proboscideus* from the salmon exhibits young forms with 6 to 16 joints, which when 1·5 to 4 mm. in length, exhibit the same form and posterior structure as those of *B. cordatus*. The segmentation begins close behind the head, which has of course at first, as in all *Bothriocephali*, a much smaller size than it subsequently acquires with the development of its adult structure.

That it is from fish that the dog and man are infected with *Bothriocephalus cordatus*, can, from the analogy of *B. latus*, hardly

[1] Kahane, "Anatomie von Tænia perfoliata." *Zeitschr. f. Wiss. Zool.*, Bd. xxxiv., p. 184.

[2] "Studien an Cestoden," p. 56: Halle, 1881.

admit of doubt, apart from the fact that it is these animals (along with other aquatic animals, birds, and seals) that furnish a great part of the food of the above-mentioned hosts. The infection can hardly be difficult, since, according to travellers, the Esquimaux eat the flesh either raw or but slightly cooked, and do not despise even the viscera. No part indeed is put aside as uneatable; neither care nor cleanliness characterise their cooking, and the food is eaten with gusto when it has been hardened by the frost.

Bothriocephalus liguloides, Leuckart.

Ligula Mansoni, Cobbold.

Cobbold, "Description of Ligula Mansoni, a new Human Cestode," *Journ. Linn. Soc. Lond.* (Zool.), vol. xvii., p. 78, (with woodcut) 1883.

This worm, hitherto observed only in the larval form, exhibits in this state a ribbon-like unsegmented body of a somewhat fleshy consistency. It attains a length of 20 cm. and more, and has a median breadth of 2·5 mm. Posteriorly the worm becomes somewhat narrower, while anteriorly it is for a short distance widened into a sort of disc. The anterior margin, which is otherwise rounded, bears in the middle a papilliform elevation, on which the head proper is borne. The latter has a somewhat compressed form, but is usually more or less completely invaginated. No sexual organs are present, nor is there any perceptible difference between the two surfaces of the body. The body is traversed by irregular wrinkles, chiefly transverse, but partly also longitudinal, which probably result from the state of preservation.

The normal habitat of the worm is the subperitoneal connective tissue of man, especially, it seems, in the lumbar region. It has been hitherto found only in China and Japan.

The first notice of the existence and occurrence of this peculiar parasite is due to Dr. Manson of Amoy, whom we have recently had to thank for a series of interesting observations on *Filaria sanguinis*. No fewer than twelve specimens were found in the body of a Chinaman, who died from dysentery and ulcerating stricture of the œsophagus (after an operation for elephantiasis of the scrotum). With the exception of a single worm, which lay free in the right pleural cavity, the parasites were all found in the region of the fossa iliaca behind the kidneys, embedded in the subperitoneal connective tissue.[1] Some were coiled up, and others more or less extended. They measured in the fresh state 30 to 35 cm.,[2] were of a dead white

[1] The history of the patient is given in the *Lancet*, 14th Oct. 1882.

[2] Cobbold gives the length of the specimens preserved in spirits as 1·2 to 3·3 inches.

colour, and exhibited when removed from their resting-place distinct tapeworm-like movements.

FIG. 402.—*Bothriocephalus liguloides*; *A*, original, *B*, after Cobbold (nat. size).

Before the publication of this notice, and the accompanying communication of Cobbold, to whom Manson sent his worms for closer investigation, I also obtained a specimen of this worm through the kindness of Dr. Scheube, then director of the hospital in Kioto, now physician in Gera. These were derived from a Japanese, twenty-eight years of age, who had been five years in prison, but was formerly for some years a groom in the island of Kiushiu, and had moved about in the west of the main island. During his residence in Kiushiu, he suffered after a prolonged careless life from hæmaturia. He became afterwards syphilitic, and remained so till his imprisonment. After he had been five years in prison his left testis began to swell and become painful. At the same time a diffuse hardening of the skin set in, on the upper part of the left thigh, below the inguinal region, and pains extended thence to the left hypochondrium. Afterwards the hardening and the pain decreased, and wholly disappeared for some months, during which the patient, in spite of the continuous slight enlargement of the left testis, felt quite healthy. In the course of a year, without apparent occasion, dysuria set in, associated with pains in the urethra and bladder. The urine itself exhibited no striking change. After the dysuria had lasted for some days, the patient observed when making water the projection of a white thread-like body, which moved when touched. He recognised it as a worm, and attempted to extricate it by winding it round a bamboo rod. After he had drawn out about 18·5 cm. in this fashion, the worm broke. The pain of urinating was temporarily relieved, but after a short period returned. The urine could only be expelled in drops by strong pressure, and with violent pains, which extended to the upper thigh. The urine was slightly cloudy, but on microscopic examination, revealed nothing unusual except blood corpuscles. Whether further portions of the worm were expelled is not known, as the patient very soon returned from the hospital to the prison.

The worm, which in spirit had contracted to 13 cm., turned out

to be an unusually long larva of a species of *Bothriocephalus*, identical with the form which Cobbold had just ranked among the human Entozoa, under the title *Ligula Mansoni*. From Manson's report, it seems clear that its occurrence in the urethra in Scheube's case was secondary. The worm does not live, as one might expect from the above, in the renal cavities, but is primarily, like the other larvæ of *Bothriocephalus*, embedded in the connective tissue of the host,—probably, as in Manson's case, in the neighbourhood of the kidneys, whence it had found its way, after further growth, into the urethra. That it is able, to some extent at least, to change its position, is evident from the fact that in Manson's case one specimen was found in the pleura; while Braun's observations on the bladder-worms from the pike (p. 726) establish the occurrence of an occasional migration. The loose nature of the enveloping sheath, and the ease with which larvæ of *Bothriocephalus* protrude their heads (as I observed on a living form 6 cm. long, taken from the subdermal connective tissue of a Japanese giant salamander), make the mechanical possibility of this wandering readily intelligible. A passage into the ureter must be less difficult for this form than for certain intestinal parasites, which also occasionally make their exit in a similar manner. I refer not only to the Ascarides, although they furnish the greater number of such instances, but also to tape-worms which in larger or smaller fragments have been evacuted with the urine (p. 486).

A new case of this kind has since been communicated to me by Dr. Noll in Hanau. A patient was taken to the hospital there on account of hæmorrhage from the urethra, and some days later, with comparatively slight pain, expelled with the urine some living proglottides, which I identified as those of *Tænia saginata*. None were to be found in the stools.

It remains doubtful whether the abnormal symptoms exhibited by the patient in Scheube's case before passing the worm were due to the wandering of the parasite into the ureter, or were to be regarded as the consequence of syphilis; equally doubtful, too, was the time and the manner of transmission. We cannot, however, be mistaken in supposing that it was a case of straying on the part of the worm, and that the latter was at first lodged, as in Manson's case, in the peritoneum.

Cobbold considers the worm as a *Ligula*, even affirming that it is nearer to *L. simplicissima*, which occurs so abundantly in our river fishes, than to any other Cestode form, though he does not exactly go the length of declaring it merely a variety of the former. I am sorry to be forced to contradict my esteemed fellow-worker and friend. The resemblance between this form and *Ligula*, especially *L. simplicissima*,

is restricted to a mere similarity of external shape. The internal structure is so different that a collation of the two seems almost impossible. Not only does *L. simplicissima*, though generally a larva like the present form, contain already well-developed reproductive organs, which attain full maturity a few days after their transference to the final host, but the histological structure of the ribbon-like body, and especially the disposition of the musculature, is thoroughly different.[1] It has, besides, to be remembered that *Ligula*, *i.e.*, the true *Ligula*, whose representative is *L. simplicissima*, is in its intermediate stage found exclusively in fishes. I speak designedly of the true *Ligula*, for this name has been frequently bestowed by helminthologists on the intermediate stages of *Bothriocephalus*, and especially on those which are characterised by the possession of a long ribbon-like body, which in its external appearance recalls to some extent the strap-worms of fishes. This is especially true of those forms which Diesing has included in his well-known "Systema Helminthum"[2] under the title of *Ligula reptans*, although, from variations in their size (in some cases a foot long), and from the variety of their hosts, they would seem to be representatives of very different species. So far as Diesing knew them, these forms were all derived from parasites occurring in various animals (mammals, birds, reptiles, and especially snakes), usually in the connective tissue of the hypodermis and of the muscles, and in snakes frequently free in the body-cavity, or below the peritoneal membrane. I have examined a number of these worms (among them one from *Lutra brasiliensis*, which Diesing also cites, a second from a Floridan bird, and a third from *Cryptobranchus japonicus*), and can distinctly affirm that they are not Ligulidæ, but, like *Bothriocephalus liguloides*, represent the young stages of certain Bothriocephalidæ. Diesing himself afterwards referred his *Ligula reptans*, with some related forms, to a specially erected genus, *Sparganum*,[3] and expressly described them as larval stages of *Dibothrium*, Diesing (= *Bothriocephalus*).[4] Cobbold also, in describing his *Ligula Mansoni*, recalls the *Ligula reptans* and the *L. nodosa* of the trout (p. 715), associated by Bertolus with *B. latus*, and has no hesitation in regarding his worm as a larval form, and even thinks it possible that it may originate from *B. latus*, so that its occurrence in man would be comparable with that of *Cysticercus*. On the whole, however, he is more

[1] See especially the inaugural dissertation of my pupil Kiessling, "Ueber den inneren Bau des Schistocephalus dimorphus u. Ligula simplicissima," *Archiv f. Naturgesch.*, Jahrg. xlviii., Bd. i., p. 241, 1882.

[2] Vol. i., p. 581.

[3] "Ueber eine naturgemässe Vertheilung der Cephalocotyleen," *Sitzungsb. d. k. Akad. d. wiss. Wien*, Bd. xiii., p. 570, 1854.

[4] "Revision d. Cephalocotyleen," *ibid.*, Bd. xlviii., p. 249, 1864.

inclined to connect it with *Ligula*, especially because of the longitudinal furrow in the median line of one surface of the body, which he collates with the sulcus longitudinalis, regarded by the descriptive helminthologists as characteristic of the genus *Ligula*. To this I shall afterwards refer, only noting here that the sulcus longitudinalis of *Ligula* is brought about only by the thick ventral line of genital apertures, and cannot therefore occur in the worm under discussion, nor indeed in any of Diesing's larval genus *Sparganum*.

The parenchymatous, or, as we said in our diagnosis, fleshy consistency of this worm is chiefly the result of the connective-tissue matrix, which forms by far the greatest portion of the larval body. No cellular texture is demonstrable. It is a homogeneous mass of clear appearance, by no means compact, and resembling a gelatinous material rather than the ordinary connective tissue. The uniform appearance is only interrupted by deposits—small, tolerably abundant, uniformly scattered calcareous corpuscles—by muscle-fibres,

FIG. 403.—Transverse section through the larval body of *Bothriocephalus liguloides*.

and by vessels. Other organs, and especially generative organs, are absent, except two nerve cords, which a careful examination of cross sections reveals on the borders of the middle third of the body, as in *B. latus*. The structure of the muscular apparatus is especially characteristic in its deviation from that of the adult *Bothriocephalus*. There is no division into cortical and median layers, for there is no development of a distinct transverse or circular musculature, such as occurs in all other Cestodes. This worm possesses, indeed, numerous strong muscle-strands, but, with the exception of those beneath the cuticle, they all run longitudinally, and never combine in large masses. Single bundles, formed by the grouping of fine refringent fibres, run parallel to one another, separated by larger or smaller intervals. These bundles are thickest near the nerve cords, where the parenchyma is more compact, forming distinct longitudinal strands,[1] which can be traced in transverse sections along the whole length of the body. We have here the explanation of the fact that the middle of the body-surface,

[1] It was apparently in reference to these longitudinal tracts that Diesing said of his *Ligula reptans* (*loc. cit.*)—"Tractus intestinalis bipartiti crura parallela in nonnullis saltem individuis conspicua."

between these strands, is often caused to sink in on either side by the action of dehydrating fluids. To the longitudinal furrow of variable length which thus results, Cobbold has erroneously attached too much importance. Similar, usually smaller, furrows are not unfrequently formed, as Cobbold has also figured, on the outer side of the muscle-strands. On the broad anterior end of my specimens there were a number of longitudinal furrows, which, as was shown by examination of similar stages in other species (I was unwilling to sacrifice my single specimen of *Sparganum* from the human subject), were associated with the muscle-bundles into a number of stronger strands, serving apparently for the retraction of the head (Fig. 390, *A*). While these muscle-bundles extend within the parenchyma for a long distance without special change, they exhibit on the surface of the worm, below the usual cuticle, a marked deviation, repeatedly dividing, ramifying, and reuniting to form a more or less regular plexus, the strands of which often pursue a transverse course, and thus replace the otherwise absent circular muscles. With these strong bundles numerous isolated fibres are associated, which branch off from the former, dividing here and there, and penetrating the clear parenchyma at intervals in all three dimensions of space. By their fineness and isolated course they recall the sagittal fibres in the muscular layer of the *Tæniæ*, except that they extend not only dorso-ventrally, but also transversely and longitudinally.

In contrast to the generally weakly developed musculature, the vascular apparatus attains considerable development. In investigating preserved specimens of *Bothriocephalus latus* and *B. cordatus* traces of the excretory system are only occasionally seen; in this worm, however, a section cannot be made in any direction without exhibiting numerous vessels of considerable calibre. In transverse sections alone some thirty can be counted without difficulty. They are, of course, especially sections of longitudinal vessels, which are, as is well known, much more abundant in the Bothriocephalidæ than in the Tæniadæ, and which penetrate the parenchyma of the body superficially as well as deeply. They seem to be specially developed near the nerve cords and the adjacent longitudinal muscle-strands. It is not, however, merely in the number of longitudinal vessels that the vascular system of this worm recalls that of *Bothriocephalus*, but also in the splitting and anastomosis by which a distinct network is formed, with meshes of considerable but variable width, and usually of rhombic form. The vessels have no special external walls; their boundaries are formed by the common ground substance, so that they are to be considered merely as lacunar passages. In spite of this, the fine muscular fibres are not unfrequently disposed in a distinctly developed annular

manner, which is probably not without influence on the width of the vascular spaces.

The great histological differences between the ribbon-shaped body of this worm and the subsequent chain, furnish sufficient evidence that the former is not directly metamorphosed into the latter, but, like the body of *Cysticercus fasciolaris*, is lost in the transition to the final state, and is replaced by a new formation. The same is probably true of related forms with longer larval bodies. In all probability the head and the immediately adjacent portion persist to form the origin of the jointed body.

The constitution of the head is but little known. Cobbold gives no report on the subject; his specimens apparently had their heads wholly retracted, and in mine the latter is only half protruded. So much, however, I may affirm, that the head has an unusually compact appearance. It appears in my specimen as an almost hemispherical protrusion, which is traversed on either side by a superficial furrow. Both furrows can be traced to the hole occupying the apex of the protrusion, and are therefore not free throughout their whole length. There are no distinct lips unless one can so regard the ridge-like protruding boundaries of the furrow. The state of affairs further forward I was forced to leave undecided.

FIG. 404. — Head of *Bothriocephalus liguloides*. (× 5.)

The life-history also of this parasite is still unknown. We are left to mere conjectures that the host of the adult worm is a carnivorous animal which comes into close association with man. It may be likewise presumed that man is not the only host of this form. It seems likely that the dog or cat, or even the pig,[1] is in some way implicated in the history of this parasite. That it occurs also in cold-blooded animals is, considering the great difference in the conditions of life, as probable as the supposition that the host of the adult worm is likewise cold-blooded.

[1] The pig is not, indeed, a domestic animal throughout Japan, but, according to my Japanese pupils, is kept in the island Kiushiu, where the host above referred to was probably infected, and in the whole province of Satsuma, to which the island belongs.

INDEXES.

GENERAL INDEX.

[INDEX OF AUTHORITIES.

LIST OF AUTHORITIES.

ERRATA.

Page 37, explanation of Fig. 24, *for* "*Echinobothrium*" *read* "*Echeneibothrium.*"
Page 140, line 11 from below, *for* "conjunction" *read* "conjunctiva."
Page 377, line 9 from below, *for* "*Spargarum*" *read* "*Sparganum.*"
Page 388, line 7 from below, after "*Tetrarhynchi*" insert a parenthesis.
Page 568, line 7, *for* "structure" *read* "uterus."
Page 490, line 22, *for* "of the Bladder-worm" *read* "from the Bladder-worm."